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Growth Responses of Great Basin Plant Species to Variation in Nitrogen Availability

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GROWTH RESPONSES OF GREAT BASIN PLANT SPECIES TO VARIATION IN NITROGEN AVAILABILITY

by

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ABSTRACT

Growth Responses of Great Basin Plant Species

to Variation in Nitrogen Availability

by

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Utah State University, 1996

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For this dissertation, I examined the ability of field-grown plants to capture N presented in enriched patches or in whole-plant pulses. I assessed root proliferation in N-enriched patches when *Agropyron desertorum* plants had been previously fertilized or shaded. All plants responded with increased root growth rates in N-enriched patches. However, root proliferation by shaded plants was 50% less than unshaded plants. Unexpectedly, plants with higher N status had greater root growth rates in enriched patches than plants that had not received N supplement. I concluded that plants already under competitive pressure above ground for light and below ground for nutrients should be less able to respond to opportunities presented in nutrient patches.

I then examined plant growth responses and biomass production of six Great Basin species (*Bromus tectorum*, *Taeniatherum medusae*, *Agropyron desertorum*,

Pseudoroegneria spicata, *Artemisia tridentata*, and *Chrysothamnus nauseosus*) following a pulse of N applied in the early, mid, or late spring. An equal quantity of N, applied continuously, was a control. Surprisingly, most of the species grown under the continuous supply had lower growth rates and less biomass production than plants recieving an N pulse. The exception was *Chrysothamnus*, which responded equivalently to all treatments. Generally, the greatest response occurred in early phenological stages. Four of the six species had their greatest response to the early-spring pulse, suggesting that these cold-season species are well-adapted to take advantage of early spring nutrient pulses. This study demonstrated that instead of benefitting from a season-long supply of N, there were times during the growing season when plants were able to use pulses of N for significant gains in biomass. I also investigated the root properties (root biomass, specific root length [the ratio of root length:root mass], and root uptake capacity) that determined plant response to pulses. Despite considerable temperature differences and changes in plant phenological stages, root uptake capacity remained remarkably constant throughout the season. However, this consistency did not explain the differences in productivity during the season. Root biomass also did not explain these growth responses to pulses. Instead, I suggest that the quantity of actively growing fine roots, plus the ability to effectively exploit the soil volume in the early spring, results in capture of early nutrient pulses.

(142 pages)

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Carol J. Bilbrough

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CHAPTER I

INTRODUCTION

Although limitation in water availability is commonly recognized as a primary factor regulating community structure and productivity in the Great Basin, nitrogen (N) is also recognized as an important secondary regulator (Crawford and Gosz 1982, West 1991). Many Great Basin species are cold-season adapted, and grow during the early spring when soils have been recently recharged from snow melt and spring rains (Dobrowolski et al. 1990). Therefore, when plant growth is most vigorous and nutrient demand high, moisture may not be limiting, and growth will be limited by nutrient availability. N availability changes spatially over scales that are relevant to individual plants (Jackson and Caldwell 1993), and temporally throughout the growing season (e.g., Burke et al. 1989). Thus, plants must be able to exploit a N resource that is variable in both space and time. The exploitation of soil N by individual plants is determined by species-specific characteristics such as timing of growth and phenological stage, as well as plant demand for N. Other factors, such as temperature, soil moisture, and light availability, also affect the ability of plants to take up soil N.

In this dissertation I examine the ability of field-grown plants to capture N presented in localized patches or in whole-plant pulses. In my first experiment, I manipulated plant demand for N through shading and fertilizing treatments, and then measured root growth responses to a localized N supply. The second and third experiments investigated the interaction between the timing of an N pulse and the ability of different growth forms and species to exploit different pulses. I examined first plant

growth responses to pulses of N and then examined the root properties that determined these responses.

PLANT RESPONSES TO N PATCHES

In Chapter II, I present the results from an experiment investigating root growth rates of plants in response to spatial variability in N availability, and how this response is affected by changes in plant demand for N. I manipulated plant demand for N by enhancing plant N status through fertilization, and by lowering both demand for N and energy supply from photosynthesis for N uptake through a shading treatment. Following these whole-plant manipulations, I created N-enriched microsites by injecting N in a localized area behind a root observation window. I also created microsites enriched only in water as a control treatment. By mapping root growth over time in the enriched and unenriched patches, I tested whether field-grown plants proliferated roots in N-enriched patches. In addition, I assessed the effects of changes in plant demand for N on these root growth-rate responses.

PLANT RESPONSES TO PULSES

How might pulses of N occur? While patterns of seasonal variability in N availability are fairly well understood (e.g,. Charley and West 1975, Burke et al. 1989, Schimel et al. 1989), little is known about the nature and timing of N pulses that may occur over shorter time scales. N availability to plants may be particularly dynamic in the

shallow portions of the soil profile that are more affected by temperature fluctuations and rainfall patterns, and that contain most of the soil organic material. Moisture and temperature affect the physiological processes of the soil microbe community, and fluctuations in these processes result in variability in NO_3^- and NH_4^+ pool sizes and flux rates through these inorganic N pools. Litter quality, quantity, and the timing of litter deposition affect plant N availability by determining substrate quality and quantity through time. In addition, there may be instances when the conditions for nutrient pulses occur relatively rapidly for a short duration. For example, wetting and drying cycles have been shown to cause fluctuations in soil mineral N concentrations (Campbell 1978, Stevenson 1986). Rainfall events, snow melt, and freeze/thaw conditions may also result in the release of nutrients through increased nutrient mobility, leaching, nutrient release, and/or stimulated mineralization (Steinberger and Whitford 1988, Stevenson 1986, DeLucia et al. 1992). These fluctuations in N availability are largely undetected due to the time scales normally measured, and are largely theoretical and speculative. Nonetheless, these pulses could be potentially important sources of N for plants.

Although it has been speculated that plants are adapted to utilize resources in pulses through responses in root growth and uptake rates (Bloom et al. 1985, Chapin 1988, Chapin et al. 1990), this has never been tested. The evidence presented above suggests that nutrient pulses commonly occur. Related studies investigating plant responses to sudden increases in localized nutrient supply (e.g., Drew and Saker 1975, Jackson and Caldwell 1989, Campbell and Grime 1989) and responses to changes in

nutrient supply following either nutrient starvation or excess supply (Lee and Rudge 1986, Robinson 1994) suggest that plants are capable of effectively utilizing ephemeral nutrient pulses. These responses may include elevated root uptake capacity and increased soil exploitation through root proliferation. The ability of plants to effectively capture nutrient pulses may ultimately contribute to plant productivity, survival, and reproduction.

In Chapters III and IV, I present the results from two experiments investigating plant responses to pulses of N. In order to study the effect of short-term pulses on plants without the confounding effects of natural pulses, I established four sand-filled replicate plots (5 x 18 m) and planted six study species in monoculture subplots. This experiment included six species (*Bromus tectorum, Taeniatherum caput-medusae*, *Agropyron desertorum*, *Pseudoroegneria spicata*, *Artemisia tridentata* ssp.*vaseyana*, and *Chrysothamnus nauseosus*) in three growth forms: annual grass, perennial bunch grass, and woody shrub. For each experiment, I applied three 4-day-long pulses in the spring (early, mid, and late spring) to different treatment plots, plus a control, continuous N supply of an equal quantity of N as one pulse for a 10-week period. In the first experiment, presented in Chapter III, I examined the effect of pulses on plant productivity. Specifically, I measured leaf tissue N concentrations, root and shoot growth rates, and root and shoot biomass at the end of the growing season. I tested the hypothesis that plants receiving a continuous supply of N would be more productive than plants receiving N in a single pulse. In addition, I predicted that the ability to exploit pulses of N would be different for different species and would vary among pulses for each species.

In the second pulse experiment, presented in Chapter IV, I repeated the same pulses and measured root properties that might explain the plant responses that were detected in the previous experiment. I used four of the six study species, *Agropyron*, *Pseudoroegneria*, *Artemisia*, and *Chrysothamnus*. Root properties included root biomass, specific root length (root length per unit root mass, SRL), and root uptake capacity. I measured root biomass and SRL at the time a pulse occurred in order to assess the root system characters at the time of a pulse, and root uptake capacity before and after pulses to determine both the capacity of the plant at the time a pulse was perceived, and to measure the effect of each pulse on root uptake rates. I predicted that the root properties that were important in capturing pulses of N would vary between species and over the course of the growing season. I also predicted that uptake capacity would be low in the spring, when soil and air temperatures were cool, and light availability less than later in the season.

In the last chapter, I present a summary of the results from Chapters two through four. A synthesis of these results, with general conclusions concerning the importance of heterogeneity of N availability, is also included. Finally, I present some suggestions for future research.

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CHAPTER II

THE EFFECTS OF SHADING AND N STATUS ON ROOT PROLIFERATION IN NUTRIENT PATCHES BY THE PERENNIAL GRASS *AGROPYRON DESERTORUM* IN THE FIELD[1]

Abstract. Competition for light can affect the exploitation of spatial heterogeneity in soil resources. To evaluate the influence of shoot status on root growth responses in nutrient-rich soil patches, we studied the effects of shading and whole-plant nitrogen status on root growth in N-enriched and nonenriched patches by mature *Agropyron desertorum* plants growing in the field with belowground competition. Roots in enriched patches had greater length to weight ratios (specific root length, SRL), indicating increased absorptive surface areas, compared with roots in control patches. Increased SRL was due to increased production and length of higher order laterals rather than morphological changes in roots of the same branching order. Although the pattern of root growth rates in patches was the same for shaded and unshaded plants, the magnitude of this response to enriched patches was damped by shading. Root relative growth rates (RGR) in N-enriched patches were reduced by more than 50% by short-term shading treatments (60% reduction in photosynthetic flux density), while root RGR in unenriched patches were unaffected by shading. Unexpectedly, plants with higher nitrogen status had greater root RGR in enriched patches than plants that had not received nitrogen

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[1] Coauthored by Carol Bilbrough and Martyn M. Caldwell.

supplement, again with no detectable effect on root RGR in the unenriched patches. Therefore, both shading and plant N status affected the ability of roots to exploit enriched patches by proliferation, but, there was no stimulation or suppression of root growth in the unenriched, control patches. Thus, plants already under competitive pressure above ground for light and below ground for nutrients should be less able to rapidly respond to opportunities presented in nutrient patches and pulses.

Introduction

Plants are exposed, through the course of their lifetime, to complex patterns of resource availability, both above and below ground. Nutrient availability varies spatially and with changing seasons, and with events such as snow melt, freezing and thawing, and precipitation. Light availability varies spatially as a result of shading by neighboring plants and temporally at several scales. Thus, plants are constantly responding to a changing mosaic of resource availability and in response to multiple interacting factors (Chapin et al. 1987; Aerts et al. 1991).

Plant responses to heterogeneous nutrient supply have been well documented. In local high-nutrient zones, root physiological uptake rates (e.g., Drew and Saker 1975,1978; Jackson et al. 1990) and root growth rates increase (e.g., Drew and Saker 1978; Granato and Raper 1989; Jackson and Caldwell 1989), often with a concomitant decrease in root growth in nutrient-poor zones (Drew 1975; Crick and Grime 1987). Increased root length in fertile patches is frequently due to increased number and length of lateral roots rather than increased growth of primary axes (Drew 1975; Granato and Raper

1989; Larigauderie and Richards 1994). However, most of the studies on root growth responses to nutrient-rich zones or patches have been conducted using seedlings under controlled environmental conditions, such as in hydroponics or in pots, where the experimental system may strongly affect root responses to nutrient patches. Also, many of these studies compared the responses of plants whose roots were distributed in a combination of enriched and deficient zones with control plants that were either amply supplied or deficient in nutrients (Robinson 1994). Thus, while these studies document potential plant responses, it is unclear how well these responses reflect root growth responses of mature plants growing under more natural circumstances.

Few studies have addressed root responses to nutrient patches by mature field-grown plants. Under field conditions, root proliferation responses are variable and depend upon factors such as the duration and timing of a nutrient patch (Pregitzer et al. 1993), seasonality and phenological stage (Eissenstat and Caldwell 1988), and presence of neighboring plant roots (Caldwell et al. 1991). In the Great Basin, neighboring plants may shade one another when the sun is lower in the sky, i.e., in the early morning or late evening, or in the early spring or late fall. Such shading reduces plant carbon available for the considerable belowground biomass of these perennial species. The consequences of aboveground competition for light can be particularly important in many ecosystems where belowground competition is severe (Remison and Snaydon 1980; West 1988; Wilson 1988). Shading reduces root growth responses for a variety of species (Robinson 1994), and Jackson and Caldwell (1992) found that shading reduced the ability of the

perennial tussock grass *Agropyron desertorum* to increase root nutrient uptake capacity in enriched nutrient patches in the field.

Differences in plant nitrogen status, as indicated by tissue N concentration, can also result in changes in plant carbon balance and nutrient demand. For example, plants with lower nutrient status exhibited greater root growth in enriched patches than did plants with higher nutrient status in pot (Philipson and Coutts 1977; Friend et al. 1990) and hydroponic (Lee and Rudge 1986) experiments. However, these responses were not tested in the field.

In this field study, we evaluated the effects of shading and plant N status on the timing, magnitude, and morphological manifestations of root proliferation in enriched nitrogen patches by the perennial tussock grass *Agropyron desertorum* (Fisch. ex Link). This grass was introduced from Eurasia into North America in the early 1900s and has been widely seeded in rangelands in the Intermountain West (Dillman 1946). In our study, shading reduced root growth responses by more than 50% compared to plants growing in full sunlight. Surprisingly, plants with higher N status had higher growth responses than plants with lower N status.

Materials and Methods

Study area

The research was conducted in the spring of 1992 at the Green Canyon Ecological Research Center (41°45'N, 111°48'W, 1460m a.s.l.; Caldwell et al. 1983). The native vegetation of the area is dominated by Pseudoroegneria spicata and *Artemisia tridentata*,

and is typical of areas where *Agropyron desertorum* has been planted. The soils are rocky mollisols (Typic Haploxerolls) which formed on alluvial fan material (Southard et al. 1978). These soils typically contain less than 10 ppm bicarbonate exchangeable phosphate, 100-200 ppm available potassium, and 5-10 ppm available NO_3 and NH_4 (Jackson and Caldwell 1991). Winter and spring precipitation was 234 mm the year of this study, considerably less than the average of 363 mm. Monoculture plots of 10-year-old *Agropyron* plants established in 1981 with a uniform spacing of 0.5 m between each plant were used for the experiment. The plants were spaced sufficiently that no aboveground competition occurred. There was competition below ground as indicated by greater growth of border plants with fewer neighbors.

Procedure

Forty plants were selected with at least two untreated plants located between each experimental plant. One root observation window (50 cm long X 30 cm high, 20° from vertical) was installed in the early spring approximately 10 cm from the edge of the crown of each experimental tussock. A small amount of sieved soil was tightly packed between the window and the field soil to fill in voids between the cut soil and the window. Some of the roots growing in the observation windows may have belonged to neighboring plants. However, the observation windows were placed very close to experimental tussocks, and the presence of the windows provided a barrier to most of the neighboring plant roots. Thus, the great preponderance of roots appearing in the windows belonged to the target plants.

Whole-plant pretreatments were randomly assigned to individual plants in a two-way factorial design with two levels of nitrogen application (unfertilized and N fertilization), and two levels of light (unshaded and shaded). In order to create a pronounced difference between the unfertilized and fertilized plants, N fertilization treatments were applied early in the growing season when plants were just beginning shoot growth, and then repeated 1 month later. For the fertilization treatment, 6 liters of 15 mM NH_4NO_3 were applied in two 3-liter applications on sequential days around the base of each plant (approximately 25 kg ha^{-1}). The unfertilized treatment consisted of 6 liters of water without nutrients. Soil extractable N was measured 1 week following each N application, and at the time of patch application. The N fertilization resulted in a measurable increase in soil N (mean of 52.3 vs 4.99 ppm total N); however, this difference was no longer detectable at the time of patch application. Shade treatments were applied 5 days prior to patch application by placing a cylinder of wire fencing covered with shade cloth over the plants, resulting in a 60% reduction in photosynthetic flux density (PFD, 400-700 nm). Daily PFD maxima reached 800 umol photons m^{-2} s^{-1} in the shaded treatments and 2000 umol photons m^{-2} s^{-1} in the unshaded treatments. Caldwell et al. (1983) demonstrated that entire *Agropyron* tussocks reached light saturation at 1200 uM photons m^{-2} s^{-1}. Thus, this shade treatment represented a substantial reduction in PFD, even at the daily maximum.

Following window installation, the plants were allowed to grow until sufficient roots were visible in the windows for mapping root growth (2 months). To determine

pre-patch root relative growth rates (RGR), roots were mapped 4 days prior to, and on the day of patch application. Each window, and therefore each plant, received two patch treatments. Unenriched (control) and N-enriched patches were randomly assigned to either side of each window. Patches of 150 ml of distilled water (unenriched) or 150 ml of 45 mM NH_4NO_3 were applied by infusing solution into the soil using wicks to a depth of 30 cm, creating a patch approximately 10 cm in diameter at the window. Patches were located 1 cm behind the window and 10 cm from the window edge and were separated by 20 cm. Patches were applied to 10 plants per day, over a course of four days. New root growth was mapped every 4 days for 20 days, with 10 plants being mapped each day for 24 days. Root tracings were digitized to determine root lengths, and then converted to RGR:

$$RGR = [\ln(L_2)-\ln(L_1)]/(t_2-t_1),$$

where L_1 and L_2 are root lengths at time 1 (t_1) and time 2 (t_2), respectively.

For root morphological measurements, roots were harvested after mapping was completed, spread on transparent sheets, photocopied, and then dried and weighed. The photocopied roots were digitized to determine the ratio of root length to mass (specific root length, SRL) and to quantify root branching patterns, specifically the number and length of lateral and sublateral roots on the main root axis. These morphological measurements were collected only for the high-N plants, since their roots exhibited the greatest responses to patches and light treatments.

The effects of the whole-plant nitrogen and shade pretreatments were assessed

prior to application of the patches. All tillers on experimental plants were counted, classed by size, and subsampled to estimate total aboveground plant biomass. Tissue samples were immediately frozen in liquid N for tissue N analysis (modified Kjeldahl, Jones et al. 1991), and leaf disks were taken to determine specific leaf area, leaf mass/area (SLA).

Analysis

Plant biomass, tissue N, and SLA were analyzed using a two-factor ANOVA, with two levels (fertilized, unfertilized and shaded, unshaded) of each factor using Number Cruncher Statistical System (Hintze 1987). Root RGR was tested using a general linear model (SAS 1985) with one continuous variable (initial root length, IRL) and four categorical variables (fertilization, shade, patch, time). Initial root length was treated as a covariate in the model because of the strong effect on root RGR. For the categorical variables, the design was a split plot, with the whole-plot factors being the plant-level pretreatments of fertilization level and light level. Patch type (unenriched, enriched) was the split-plot factor. Because the assumptions of correlation between time observations for univariate repeated measures methods were not met, the repeated measures portion of the analysis was conducted using a multivariate technique.

Results

Nitrogen and shade pretreatment effects

The nitrogen fertilization pretreatment did not consistently result in larger plants (Fig. 1A), although tissue N concentrations were significantly increased (Fig. 1B,

P=0.0019). The shaded, unfertilized plants were significantly smaller (P=0.007) than plants in the other treatment combinations. However, the shading pretreatment was applied immediately prior to the biomass measurements and the plants were at peak biomass. Therefore shading did not cause this difference. Instead, this treatment difference is the result of randomly assigning plants to treatments in the early spring before plant growth had begun, which resulted in inadequate dispersion of different-sized plants. Plant biomass was not correlated with either root RGR or initial root length (IRL, P=0.58), and thus target plant biomass did not directly affect root growth responses.

Initial root length and root growth responses

Root length in the observation windows at the time of patch application inversely affected root proliferation responses (Table 1, P<0.0001). Plants with lower IRL in the windows exhibited greater growth responses than plants with higher IRL. This relationship was more pronounced in the N-enriched patches compared with the unenriched distilled-water patches, as indicated by a significant patch x IRL interaction (Table 1, P=0.0030). The significant time x IRL x patch result indicates that the nature of this relationship changed over time (Table 1, P=0.0121). To illustrate the typical relationship between root RGR and IRL, separate regressions of root RGR on IRL were computed for each patch type at day eight (Fig. 2).

Root relative growth rates

Root RGR was significantly different between patch types, with a marked response

to enriched patches but not to unenriched patches (Fig. 3, Table 1, $P<0.0001$). Regardless of pretreatment, root RGR in the unenriched patches was consistently lower than in N-enriched patches. Based on a comparison with initial root RGR at day 0, there is no evidence for either a stimulation or suppression of root growth response to the unenriched (distilled water) patches as suggested by other studies (e.g., Pregitzer et al. 1993). Additionally, there is no evidence to suggest pretreatment effects (N status or light availability) on root growth responses to distilled water patches. The pattern of root RGR over time in the N-enriched patches was consistent for all pretreatments. Increased root RGR was apparent after 4 days, with the maximum response occurring by 8 days (Fig. 3). Growth rates had declined by day 12, and appeared to be approaching control root RGR by day 20.

Shading dramatically reduced root growth responses in the N-enriched patches, with a reduction of more than 50% in maximum root RGR (Fig. 3). While the effects of plant N status were less dramatic, fertilized plants had greater root RGR in N-enriched patches than unfertilized plants (Fig. 3). By day 8, fertilized plants had root RGR that were 5 times greater in N-enriched patches than in unenriched patches, while root RGR of unfertilized plants were only 3.6 times greater than that of the controls. While this pattern also holds for the shaded plants, the difference in root RGR between fertilized and unfertilized plants was considerably damped, with no proportionate difference in response between unenriched and enriched patches in the two levels of N pretreatment on the 8th

day. Thus, when plants were shaded, nitrogen status had less effect on root proliferation responses.

Root morphological responses

Specific root length (SRL) in the N-enriched patches was greater than in the unenriched patches regardless of light pretreatment (Fig. 4, P=0.003), indicating that the enriched patches had greater root length, and thus absorbing surface per unit biomass, than roots in the unenriched patches. The number of lateral root branches was not different between patch types, although the mean length of lateral roots was significantly greater in the enriched than in unenriched patches (Fig. 5 A&C). In contrast, both the number of sublaterals and mean sublateral length were greater in the enriched patches of unshaded plants, while there was no detectable difference in the shaded plants (Fig. 5 B&D).

Discussion

Field-grown *Agropyron* plants responded to N-enriched patches with increased root relative growth rates, supporting extension of the paradigm of root proliferation responses to nutrient enrichment from plants in hydroponics and pots to plants growing in more natural conditions. These results also suggest that well established, long-lived perennial plants are capable of responding to enriched patches in a manner similar to seedlings which are frequently used in controlled-environment studies. Root proliferation responses in enriched patches were clearly related to initial root length; plants with low

initial root length exhibited greater response. High local root density may cause interference to further root growth, either due to resource depletion or possibly by some interference mechanism (Mahall and Callaway 1991).

Proliferated roots in the enriched patches had high specific root length. This was primarily due to increased number and length of higher order lateral roots, which have higher length:mass ratios. There is no evidence in this study that roots of the same branching order were thinner in nutrient patches. The pattern of increased lateral root formation in response to enriched patches is consistent with other studies (Drew and Saker 1975, Granato and Raper 1989, Larigauderie and Richards 1994), although none have been done in the field. The presence of more sublateral, and thus thinner, roots in the enriched patches suggests that these roots may be more ephemeral than roots in the unenriched patches. Eissenstat (1991) found that roots with the most rapid extension rates were those with greatest SRL. Higher root mortality rates have been reported for roots in fertile patches (Gross et al. 1993) and for roots with higher SRL (Shaver and Billings 1975). Since nutrient patches are a finite resource, it would benefit the plant to produce short-lived roots with rapid growth rates to maximize exploitation of the resource patch and minimize maintenance costs of roots once the nutrients are depleted. In this case, turnover rates in enriched patches would be greater than in unenriched areas resulting in potential enhancement of nutrient availability.

Manipulation of the plants by fertilization and shading strongly affected belowground growth responses to patches. Relative to unshaded plants, shading

substantially reduced root RGR in enriched patches; however, root growth in unenriched patches was unaffected by shading. In a similar vein, Jackson and Caldwell (1992) found that root physiological uptake capacity was reduced by shading in enriched, but not in unenriched patches. The reduction in root proliferation, and possibly uptake capacity, may be due to decreased carbon supply and/or decreased nutrient demand. Although root TNC was not measured in this study, short-term shading has been shown to decrease root total nonstructural carbohydrates (TNC) and nutrient content, as well as root growth and uptake (Crapo and Ketallapper 1981; Jackson and Caldwell 1992). Thus, shading appears to rapidly reduce the ability of roots to exploit nutrient-rich patches by proliferation and possibly by increased uptake rates, while having little influence on normal growth and perhaps on uptake rates in unenriched patches.

Plants with higher N status had a greater growth response to enriched patches than lower N status plants. This seems contradictory to other studies that were conducted in hydroponic and pot systems that suggest that plants with lower nutrient status respond more strongly to enriched "patches" than higher nutrient status plants (Drew and Saker 1975, 1978; Friend et al. 1990). However, most of the hydroponic and potted-plant studies were conducted with plants in extreme nutrient deprivation or abundance. In contrast, we argue that the plants in our study were neither severely deprived nor excessively well supplied with nutrients; rather they were in a range of N-sufficiency which is more common in field situations, where carbon and nitrogen gain tend to be more

balanced (Field and Mooney 1986). Thus, plants with higher N status appear to be more vigorous and, therefore, exhibit greater growth responses.

Our results clearly show that shading and previous nutrient supply strongly affect the ability of plants to respond to heterogeneous distributions of nutrients. Shading and lower N status markedly damped the root proliferation response in nutrient-enriched patches, even though root growth in unenriched soil was not particularly affected. Thus, plants already under competitive pressure above ground for light, as simulated by our shading treatment, and below ground for nutrients should be less able to rapidly respond to opportunities for nutrients presented in patches. Roots growing in fertile patches were characterized by higher SRL, and thus greater absorbing surface area per length of root. However, this was a result of increased number and length of higher order lateral roots rather than a morphological change in roots of the same order.

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Table 1 Analysis of root relative growth rates using a general linear model. Initial root length (IRL) is a covariate, whole-plant treatments of nitrogen status (unfertilized, N fertilization) and light availability (unshaded, 60% shade) are the whole-plot factors. Patch type (unenriched, N-enriched) is the split-plot factor. Repeated measures were analyzed using MANOVA, because the assumption of univariate repeated measures were violated

Source	DF	F Value	P > F
IRL (covar)	1	48.67	0.0001
N	1	35.30	0.0001
SHADE	1	120.89	0.0001
N * SHADE	1	5.51	0.0253
ERROR [PLANT(N*SHADE)]	34		
PATCH	1	137.02	0.0001
N * PATCH	1	20.52	0.0001
SHADE * PATCH	1	59.30	0.0001
N * SHADE * PATCH	1	9.56	0.0041
IRL * PATCH	1	14.41	0.0006
ERROR	32		
Repeated Measures:			
T	4	18.308	0.0001
T * IRL	4	5.377	0.0023
T * N	4	5.740	0.0016
T * SHADE	4	14.353	0.0001
T * N * SHADE	4	1.002	0.4226
T * PATCH	4	19.032	0.0001
T * N * PATCH	4	2.891	0.0396
T * SHADE * PATCH	4	8.141	0.0002
T * S * N * P	4	1.743	0.1676
T * IRL * PATCH	4	2.209	0.0121
ERROR	29		

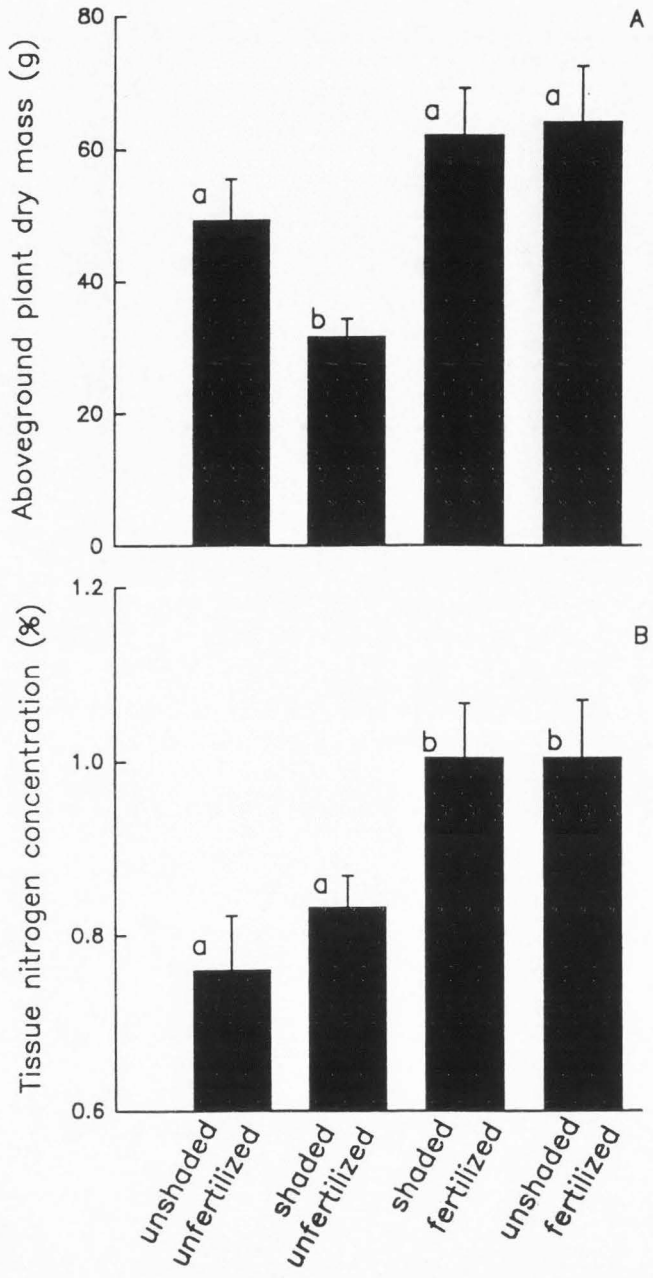

Fig. 1 A, B Effects of whole-plant N fertilization and shade pretreatments on Agropyron desertorum. A) Estimated plant biomass (mean and s.e. for n=10 plants) and B) Leaf and stem tissue N concentrations. Measurements were made one week prior to patch creation. Nitrogen fertilization treatments were applied 60 days prior to measurements, shade treatments were applied 2 days prior to measurements

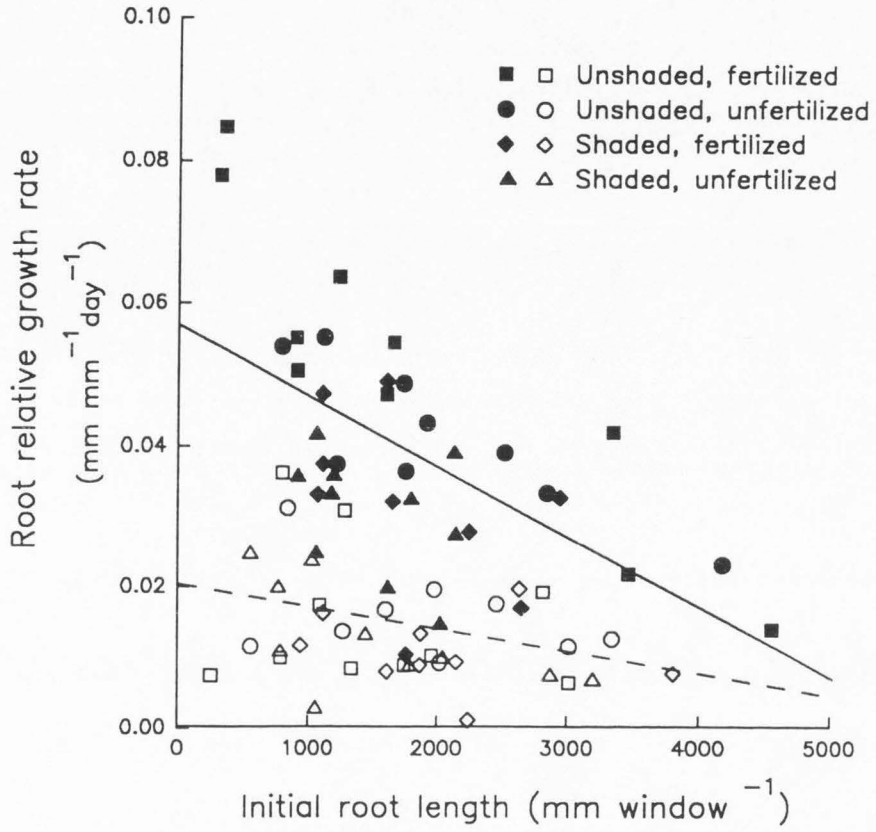

Fig. 2 The effect of initial root length on root RGR 8 days after patch creation for all treatments. Each symbol represents root RGR in one patch, for a total sample size of 80 (2 patches per plant). Unenriched (water) and enriched (NH_4NO_3) patch treatments are represented by hollow and filled symbols, respectively

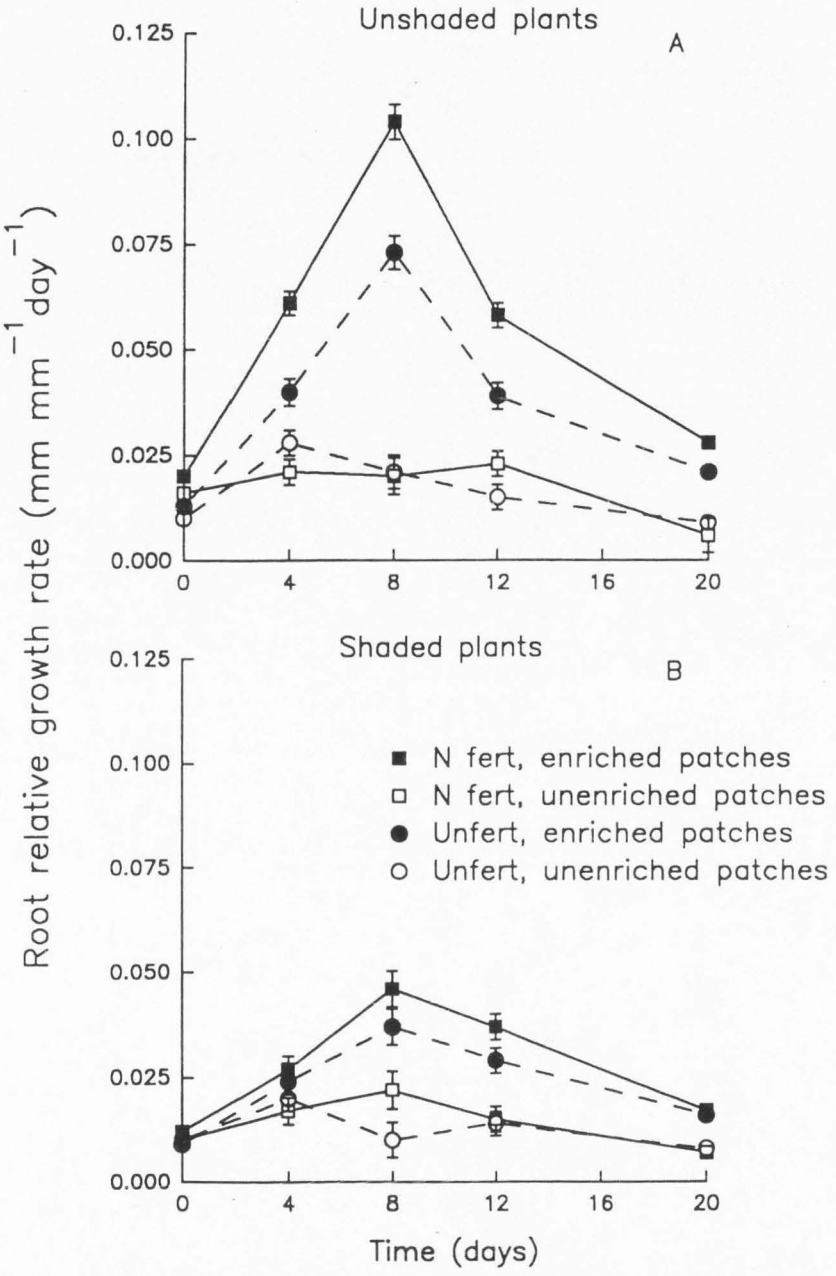

Fig. 3 A, B Mean root RGR over time in N fertilization and shade treatments in response to unenriched and NH_4NO_3 patch types. A) Unshaded treatment and B) Shade treatment, 40% PFD. The N fertilization and unfertilized treatments are represented by solid and dashed lines, respectively. Unenriched (water) and enriched (NH_4NO_3) patch treatments are represented by hollow and filled symbols, respectively. Each point is the mean and s.e. for 10 plants

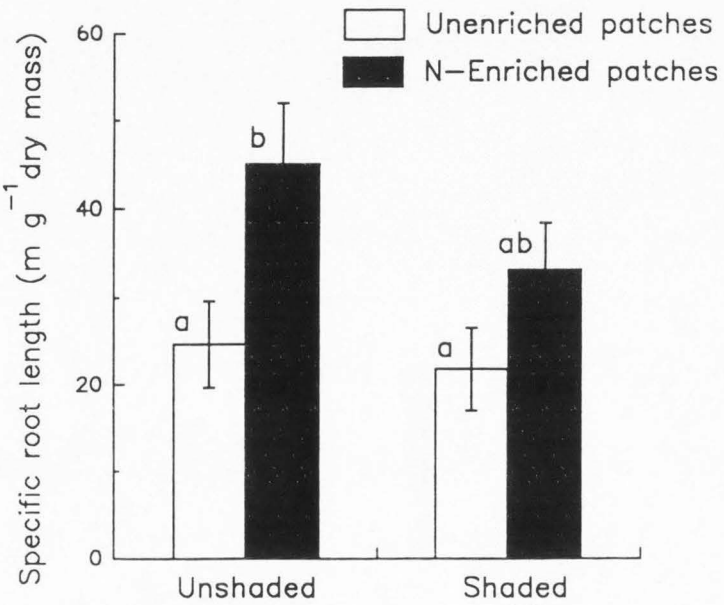

Fig. 4 Specific root length in unenriched (distilled water)-patches and enriched N patches for twenty fertilized plants growing in full sunlight or shade (40% PFD, mean and s.e., n=10 patches)

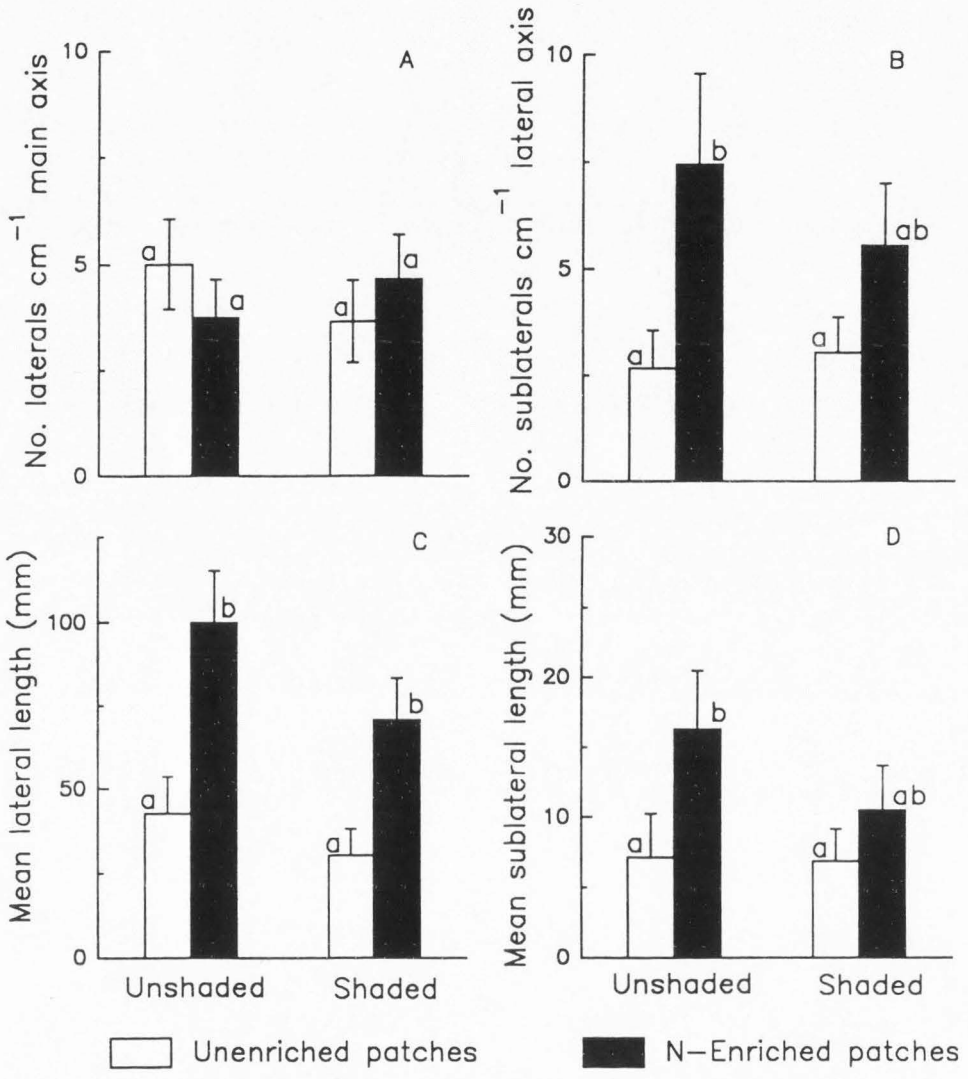

Fig. 5 Root morphological responses to unenriched (distilled water) and enriched N patches by lateral roots (a and c) and sublateral roots (b and d). Morphological responses include the number of roots produced (a and b) and new root length (c and d). Twenty plants, all from the N fertilization whole-plant treatment, but with both levels of light were used for this analysis. Each bar represents the mean and s.e. of 10 patches

CHAPTER III

EXPLOITATION OF SPRINGTIME EPHEMERAL N PULSES BY SIX GREAT BASIN PLANT SPECIES

Abstract. The ability to exploit short-duration nutrient pulses may be an important factor in the competitive balance of plants and in shaping plant community structure. We investigated the growth responses and biomass production of six Great Basin plant species growing in monocultures in the field following the application of a single pulse of nitrogen applied either in the early, mid, or late spring. As a control, we applied an equal quantity of N as was in individual pulses in a continuous manner for ten weeks in the spring. Surprisingly, most of the species grown under the control, continuous N supply had lower growth rates, fewer tillers and less biomass production than plants receiving N in a pulse. Although not all pulses increased productivity relative to controls, at least one pulse did in all but one species. The exception to this pattern was the shrub *Chrysothamnus*, which responded to all pulses and the control supply with equivalent growth rates and biomass production. Each species responded differently to the set of pulses, with the greatest response occurring early in the growth phase when plants were small and growth rates were high. Thus, phenological stage determined the timing of maximum response. Four of six species not only responded to the early-spring pulse, but had their greatest response to this pulse, suggesting that the cold-season adapted species of the Great Basin system are well-suited to take advantage of this pulse. The combination of rapid plant growth rates and predictable pulses following snow melt would likely result in intense competition

for nutrients at this time. Our study demonstrates that plants are remarkably capable of utilizing pulses of N, and that pulsed nutrients are potentially important in natural systems. Additionally, it suggests that studies conducted under constant nutrient supply may not reflect the responses of plants growing under pulsed nutrient conditions. Instead of benefitting from a season-long continuous supply of N, there were times during the growing season when plants were able to use pulses of N for significant gains in biomass.

INTRODUCTION

There is increasing awareness of the importance of temporal and spatial nonuniformity in nutrient supply and its fundamental role in plant nutrient budgets and productivity. While patterns of seasonal nutrient availability are fairly well understood (e.g., Gupta and Rorison 1975, Burke 1989), few studies have focused on temporal patterns of nutrient availability at a time scale relevant to plant response times. Nutrients are thought to often become rapidly available in short-duration pulses (Chapin et al. 1990), and these pulses are likely an important component of the annual nutrient supply for plants (Campbell and Grime 1989, Jonasson and Chapin 1991). Nutrient pulses occur as a consequence of early spring nutrient influx from the snowpack (Bowman 1992), freeze-thaw and wetting-drying cycles that lyse microbial cells and stimulate mineralization (Fisher et al. 1987, DeLuca et al. 1992, Lodge et al. 1994), and disturbances such as pocket gopher burrowing or fire. Plant responses to pulses will depend on when the pulses occur in relation to plant growth stage and environmental conditions. Thus,

because of differences among species in phenology and timing of demand, there is a complex interaction between species-specific traits and the timing of pulsed nutrients that is expected to determine the response of an individual species to a nutrient pulse.

A suite of coexisting species will usually differ in characters such as growth form, phenology, and morphological and physiological plasticity which results in a range of growth timing and ability to respond to nutrient pulses. Plants growing in the Great Basin are capable of exploiting nutrients in enriched soil patches through increased localized root growth and uptake capacity (Jackson and Caldwell 1989, Jackson et al. 1990, Caldwell et al. 1991b). These responses may occur very rapidly, within days for both proliferation (Jackson and Caldwell 1989, Bilbrough and Caldwell 1995) and changes in uptake capacity (Jackson et al. 1990). The speed of these responses suggests that these species are well equipped to exploit ephemeral pulses. However, the strength of response varies among species (Jackson and Caldwell 1989), competitive environment (Caldwell et al. 1985, Caldwell et al. 1991a), and season (Eissenstat and Caldwell 1988a, Larigauderie and Richards 1994).

Plants are capable of acquiring nutrients available in pulses (Lee et al. 1983, Bloom et al. 1985, Chapin 1988, Chapin et al. 1990, Robinson 1994). However, most of the available information comes from a few studies conducted largely on the early growth phases of herbaceous plants under controlled-environment conditions. Laboratory experiments demonstrate that plants acquire nutrients from pulses differently depending on resource availability and disturbance frequency in their normal habitats (Poorter and

Lambers 1986, Crick and Grime 1987, Campbell and Grime 1989, Miao and Bazzaz 1990) and their competitive status (Campbell et al. 1991). Controlled-environment studies also suggest that some, but not all, species altered their biomass production and allocation patterns in response to pulse timing (Benner and Bazzaz 1988, Miao and Bazzaz 1990). A field study found that phosphorus pulses were a more important resource than steady-state mineralization for *Eriophorum vaginatum* growing under natural conditions in the Arctic tundra (Jonasson and Chapin 1991). The majority of these studies have focused on the responses of plants from contrasting environments such as those of low and high nutrient availability. None have examined the range of responses to nutrient pulses by multiple species coexisting in the same system, and how these responses vary over time.

Our field study examined the ability of several plant species of the Great Basin to exploit pulses of nitrogen (N). Species chosen for this study differ in growth form and phenology. We applied equal quantities of N in pulses at three different times during the spring growing season. As a control, we provided a continuous N supply throughout the spring equal in quantity to the N in a pulse. We predicted that within a species, the magnitude of response will vary with the time of the pulse during the growing season, and that species will differ in their patterns of response to pulse timing. We also predicted that all species would have the greatest biomass production in the control treatment. As manifestations of responses to pulses, tissue N concentrations, seasonal growth patterns, and total biomass production were determined.

MATERIALS AND METHODS

Setting and species descriptions

The Great Basin is characterized by cold winters and hot, dry summers with precipitation primarily in the winter and spring. As a consequence, many plant species are adapted to grow during the early spring when snow melt and spring rains have recharged soil moisture. Alternatively, some deeply rooted species grow throughout the summer without experiencing significant water limitation (Donovan and Ehleringer 1994). While aboveground plant cover is sometimes sparse, rooting density is high. Thus, while competition for light may not always be pronounced, competition for water and nutrients is often intense (Dobrowoski et al. 1990). In this system, plants experience both regular nutrient pulses in early spring following snowmelt and unpredictable nutrient pulses from spring rains and occasional summer convection storms.

Two plant species within each of three growth forms, woody shrubs, perennial tussock grasses, and annual grasses, were chosen for study because they commonly co-occur throughout the Great Basin. *Artemisia tridentata*, ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush), is a woody shrub that may increase in abundance in severely grazed areas, where competition by the grasses is reduced due to grazing pressure and where fire frequency is not high. *Chrysothamnus nauseous* (Pallas) Britt. (rubber rabbitbrush), although ubiquitous in the Great Basin, increases substantially in disturbed systems. *Pseudoroegneria spicata* (Pursh) Love (bluebunch wheatgrass) is a native

perennial tussock grass that is intolerant of continuous grazing. Communities where *Pseudoroegneria* has been eliminated are commonly rehabilitated with the more competitive species, *Agropyron desertorum* (Fish. ex. Link) Schult. (crested wheatgrass), a perennial tussock grass introduced from Eurasia. *Bromus tectorum* L. (cheatgrass) and *Taeniatherum caput-medusae* (L.) Nevski (medusahead) are exotic winter annual grasses that have invaded the Great Basin. Both species, especially *Bromus*, have become an important ecological component of the sagebrush steppe ecosystem (Mack 1981, 1986).

This study was conducted at the Utah State University Green Canyon Research Area, located 4 km northeast of Logan, Utah (41°45'N, 111°48'W, 1460 m elev.). Mean annual precipitation is 468 mm, with much of the precipitation falling as snow in the winter. Mean annual temperature is 8° C. The growing season the year of this study began in late March and continued unusually long into late July due to low temperatures and high precipitation. The species used in this study are adapted to basic soils and conditions of low phosphorus availability due to the calcareous nature of the soils. In addition, N limitation has been demonstrated by N fertilization studies (Bilbrough and Caldwell 1995, Bilbrough, unpublished data). More information on the soils of the area is given in Jackson and Caldwell (1991) and Southard et al. (1978). This site is typical of Great Basin areas where *Artemisia*, *Chrysothamnus* and *Pseudoroegneria* naturally occur, and where *Agropyron* has been seeded (Caldwell et al. 1981). *Bromus* occurs in localized dense stands within and surrounding the research area. *Taeniatherum* is well established within Idaho and is invading into northern Utah.

Because of the potential for confoundment of a controlled-pulse experiment with the occurrence of natural N pulses, we established large sand-filled plots in the field where root growth was not confined and nutrient supply could be controlled. Four replicate 5-x-18-m plots were excavated to a depth of 1 m, and then filled with washed sand in the spring of 1992. The six study species were planted in monoculture subplots within each main sand plot during the summer and fall of 1992. Each species was planted in a pattern of six rows with plants staggered in adjacent rows and a uniform spacing between all plants. For the four replicate plots, there was a total of 1,152 plants per species. Spacing between plants necessarily varied among growth forms because of the inherent differences in plant size. Shrubs, perennial grasses, and annual grasses were planted with a spacing of 25, 20, and 5 cm, respectively. The four perennial species were arranged in parallel subplots alternating in growth form, neighboring species, and main plot location such that each of the four possible combinations of subplots occurred only once. Annual species were planted in parallel subplots at one end of each main plot. Thus, rather than randomization of species subplot locations within each main plot, subplots were disbursed with respect to location within the plots and in relation to each other. This was done because of the difficulty in obtaining adequate dispersion with randomization of a small sample size. Combinations of subplots were randomly assigned to the main plots.

Chrysothamnus and *Artemisia* shrubs were planted as one-year-old seedlings germinated from seeds collected in Utah county, Utah (Plants of the Wild, Tekoa, WA). The perennial grasses were transplanted in groups of approximately 20 tillers collected

from mature tussocks. *Pseudoroegneria* plants collected from a local population in Green Canyon and *Agropyron* plants from 13-year-old plots within the research area were used. Grasses were excavated to a depth of 30 cm, and the soil was removed from the root mass. Individual tillers with roots from three-five tussocks were then grouped for planting. Over 150 mature tussocks of each perennial grass species were required to obtain sufficient plant material, and therefore, the responses of these two species to the pulse treatments were integrated over many individuals. Annual grasses were planted as seed in the fall of 1992. *Bromus* seeds were collected from within the research area, and *Taeniatherum* seeds were collected approximately 20 km south of the research area.

Plants were fertilized three times with a commercial fertilizer (Miracle Grow, 30:30:30 NPK) at biweekly intervals during the fall of 1992 in order to facilitate establishment. Following snow melt in the spring of 1993, a modified low-N Hoaglands solution was applied weekly as background fertilization throughout the experiment to all treatments such that nutrients other than N were applied at one quarter strength of normal Hoaglands solution and at an approximate rate of 2.3 l m^{-2}. Nitrogen was added as 0.5 mM NH_4NO_3 at a rate of 0.043 g N m^{-2} (0.43 kg ha^{-1}). Plots were watered using a drip irrigation system. Plants showed no sign of nutrient or water stress throughout the course of the experiment.

Experimental design

Each monoculture subplot was divided into four treatment units 11-12 plants long

and six rows wide. Plants in the outer two rows and between treatment plots were border plants, leaving the two center rows of eight plants each as experimental plants. Treatment units were randomly assigned to one of four N addition treatments: three pulses applied during different times of the growing season and a control, continuous N supply. Pulses were applied in the early spring, May 7-10; midspring, June 4-7; and the late spring, June 25-28. The control N applications began 2 weeks prior to the first pulse on April 24 and continued 1 week after the last pulse, July 4.

Because of the inherent differences in plant sizes among species and particularly among growth forms, it was not possible to apply N in equal pulses among the species. Within a growth form, all treatments received the same quantity of N, applied either in one of three pulses or continuously over a 10-week period (control). Each pulse was delivered daily for four consecutive days in the same concentration for all species (3.6 mM N as NH_4NO_3), and with the same volume for each growth form. This was followed by a heavy watering treatment to flush the N below the major root zone. Shrubs, perennial grasses, and annual grasses received total N applications of 1.95, 2.0, and 2.7 g N m^{-2}, respectively, over the course of the 4-day pulse (corresponding to 0.093, 0.063, and 0.013 g N per plant). The control treatment consisted of 10 weekly applications of 1.4 mM N as NH_4NO_3, applied in the same manner as the pulses (corresponding to 0.093, 0.063, and 0.013 g N per plant for shrubs, perennial grasses, and annual grasses). Thus, control plants received two N applications weekly, background fertilizer N and the control N treatment. When calculated over a 4-month growing season, the amount of N added in

the treatments represented 50% of the total N added to the plots.

Measurements

Soil N was extracted using 5-cm cores from depths of 0-50 cm in subplots receiving pulses using 2 M KCl every day for 21 days beginning the day before each pulse treatment. Samples were shaken for 2 hours and filtered, and the filtrate was analyzed colorimetrically for NH_4^+ and NO_3^- with a flow-injection autoanalyzer (Lachat Instruments, Mequon, WI).

Shoot and root growth were measured on a randomly selected subsample of three equidistant plants grouped in a triangle in each treatment plot throughout the growing season, beginning April 15 and continuing through plant senescence for each species. Phenological stages (vegetative or reproductive tiller/twig growth, flowering, senescence/quiescence) were recorded when shoot measurements were taken. Root growth was measured using minirhizotrons (Richards 1984), installed vertically because the sand collapsed when attempts were made to core at an angle. One observation tube per treatment plot was located equidistant from the three experimental plants in late winter prior to root growth. Thus, the root data integrated the belowground responses of the three plants surrounding the tube. New root appearance was monitored every 2 weeks by counting new roots along lines scored around the minirhizotron tube every 5 cm from 5-50 cm in depth. These data reflected new root growth. Shoot growth was measured on the same three experimental plants. Three individual grass tillers were randomly selected

on each plant prior to the initiation of growth, and tiller height from the base of the tiller to the base of the top leaf was measured every 7-14 days. The number of tillers on each plant was also counted. For the shrubs, three twigs were randomly selected on each plant prior to growth, and the length from the previous bud scar to the base of the apical bud was measured every 7-14 days. Thus, for each treatment plot, nine tillers or twigs were measured on three plants. Subsampling increased the robustness of the treatment-level estimates of shoot growth responses.

Leaf tissue N concentrations following pulses were used as an indication of short-term plant responses to pulses. A pair of tissue N samples were collected from pulsed and control plants for each pulse ten days following the initiation of each pulse. Tillers or twigs from experimental plants, but not those used for growth measurements, were collected, immediately frozen in liquid N, and freeze-dried, and the leaf tissue was separated and ground. Total leaf tissue N was analyzed by a continuous flow direct combustion and mass spectrometry using an ANCA 2020 system (Europa Scientific Inc., Cinncinatti, OH).

Plant biomass was measured using destructive harvests. The entire shoot system was collected and root biomass was estimated by harvesting the soil volume below the plant crown to a depth of 50 cm and then subsampling the area between plants with four 10 x 50 cm cores. Three plants of each grass species were harvested at peak biomass when they were flowering and then one plant per species after senescence for assessment of seed production. Three plants of each shrub species were harvested in September when

vegetative growth was complete. No seed production measurements were collected for the shrubs since few flowered.

Analysis

Quantitative comparisons were conducted at the species level, while comparisons among species were qualitative. This is because species subplot locations were not randomized and therefore, the assumption of random sampling for statistical tests may have been violated. Within each species, where randomness, normality, and independence of treatment means were reasonable assumptions, analysis of variance procedures were performed using general linear models (SAS 1988). Box plots and normal probability plots of residuals were used to assess normality and outliers. Where appropriate, planned comparisons were conducted using Tukey's t test (pairwise comparisons) or Dunnett's test (control vs treatments) as described by Day and Quinn (1989). Statistical power was low in this experiment because of small sample sizes and high variability common to many field experiments. Accordingly, we did not rigidly adhere to the traditional standard of statistical significance at $P<0.05$. While this approach may increase the chances of Type I error (concluding treatment differences when there are none), the alternative error of concluding no treatment effect when there is one (Type II error) is reduced. The *P*-values are included, allowing readers to form their own conclusions.

Differences between pulsed and control leaf tissue N were analyzed by testing whether the difference (pulse minus control) was not equal to zero. Differences in the

magnitude of response among pulses was examined using analysis of variance. Soil N, and root and shoot growth over time were analyzed with two categorical factors (pulse, time). Because the assumptions of correlation between time observations for univariate repeated-measures methods were not met, the repeated-measures portion of the analysis was conducted using a multivariate technique. No specific comparisons were made between means in the repeated-measures analyses (Day and Quinn 1989); instead, time-x-pulse *P*-values were used to evaluate treatment effects over time. Tiller numbers and root and shoot biomass were analyzed with two factors (main plot, pulse). An estimate of initial shrub biomass was included as a covariate. Paired comparisons were made between control and pulsed plants when the overall test yielded a significant *P*-value.

RESULTS

N pulse applications

During the four-day pulse period, the daily NH_4NO_3 applications resulted in a large increase of extractable N in the sand (Fig. 6). After cessation of pulses and flushing, the sand N levels were equal to or below initial sand N (inset, Fig. 6). Although applications of NH_4^+ and NO_3^- were equal, sand NH_4^+ concentrations were consistently lower, probably due to a combination of volatilization, microbial nitrification and immobilization, and plant uptake. The pulses resulted in similar sand N values for all species and pulse treatments.

Plant phenology and timing of pulses

Plant phenology was different for each species (Fig. 7). The annual grasses typically germinate in the fall or early spring, grow in the spring, and disperse seed and die by early summer. In this study, both species germinated in the spring. *Bromus* began growth earlier and senesced earlier than *Taeniatherum*. Thus, *Bromus* was in a more active state for the early pulse and was nearly completely senesced by the time of the late pulse, while *Taeniatherum* was in the three-leaf stage during the first pulse and was still flowering at the time of the last pulse (Fig. 7). The perennial grass species typically initiate growth in the early spring, largely from overwintering tillers, produce reproductive tillers during the midspring, and then enter a dormant state following seed set in the early to midsummer. Both perennial grass species were in vegetative growth during the early-spring pulse, producing reproductive tillers during the midspring pulse, and setting seed during the late-spring pulse (Fig. 7). Thus, the phenological differences between these two species were subtle.

Artemisia is evergreen. It produces new leaves and vegetative long shoot growth in the early spring, and reproductive long shoots in the late spring that continue to grow throughout the summer. Flowering is in the fall and the plant retains foliage over winter. In this study, *Artemisia* was initiating long shoot growth and producing leaves during the first pulse, in vegetative growth during the second pulse, and producing flowering stems during the late-spring pulse (Fig. 7). *Chrysothamnus* overwinters with no leaves and has a prolonged period of bud swell and leaf production prior to long shoot growth in the

spring. Vegetative long shoot growth continues throughout the summer with flowers produced on the terminus of the long shoots in the autumn. *Chrysothamnus* was in bud swell for the early pulse, in the early stages of long shoot growth for the second pulse, and still in vegetative growth phase during the final pulse (Fig. 7).

Plant tissue nitrogen responses

Leaf tissue N concentrations 10 days after initiation of a pulse were indicative of short-term responses to a pulse. All species significantly increased leaf N concentrations following at least one pulse compared to controls (Fig. 8). However, the magnitude of response relative to the control was different for each species and for different pulses, indicating a pronounced effect of species and pulse timing. Due to their short life histories, the annual grasses only responded to two of the three pulses (Fig. 8A,B). *Bromus* had the greatest increase in tissue N concentrations following the early-spring pulse ($P<0.0001$) and a significant, but lower, response to the midspring pulse ($P<0.0001$, Fig. 8A). In contrast, *Taeniatherum* did not have higher N concentrations than controls after the early-spring pulse, but did have pronounced and nearly equal responses to the mid- and late-spring pulses ($P<0.0001$, Fig. 8B). *Pseudoroegneria* and *Agropyron* responded to all three pulses with higher tissue N concentrations than in controls ($P<0.0001$, Fig. 8C,D); however, *Pseudoroegneria* tissue N increases were greatest following the early spring pulse, while *Agropyron* response was greatest after the late spring pulse (Fig. 8C,D). *Artemisia* leaf tissue N concentrations significantly increased as

a result of early and midspring N pulses ($P \leq 0.0004$), but were not significantly different from control leaf tissue N concentrations from the late-spring pulse ($P=0.19$, Fig. 8E). *Chrysothamnus* leaf N concentrations increased in response to pulses in the mid and late spring ($P \leq 0.0005$), but not in the early spring ($P=0.77$, Fig. 8F). However, *Chrysothamnus* was beginning to produce leaves and therefore, a response may have been undetected because N was stored in tissues other than leaves. In the cases where a response was detected, there is no indication that pulses differentially affected tissue N in both shrub species. Instead, each shrub species responded to different pulses with similar increases in N concentrations ($P \geq 0.39$, in all comparisons, Fig. 8E,F).

Plant growth response

The timing and magnitude of root and shoot growth responses to pulses were different for each species and were not consistent within growth forms (Figs. 9&10). Growth responses to pulses generally continued well beyond the length of the pulse and were not always detected at the time of the pulse. New root production differed with timing of pulses in a pronounced manner (Fig. 9). *Taeniatherum* root production was highest following the mid- and late-spring pulses, with no response to the early-spring pulse relative to the control treatment (repeated measures pulse x time interaction $P<0.0001$, Fig. 9B). Although it appears that *Bromus* root production is greater in the pulsed treatments than controls, this trend is not significant ($P=0.33$, Fig. 9A). *Pseudoroegneria* dramatically increased root growth following the early-spring pulse

(pulse x time interaction $P<0.0001$, Fig. 9C). Mid- and late-spring pulses also stimulated root production, but the response was less pronounced. *Agropyron* plants also responded to the early- and midspring pulses, although there was no evidence of a growth response to the late-spring pulse (pulse x time interaction $P<0.0001$, Fig. 9D). New root production by *Artemisia* and *Chrysothamnus* was not affected by any pulse relative to control plants (pulse x time interaction $P=0.36$ *Artemisia*, $P=0.81$ *Chrysothamnus*, Fig. 9E,F).

Aboveground tiller and twig length of the control plants generally appeared to be less than that of pulsed plants (Fig. 10). However, unlike the marked root responses, few of these responses were statistically significant. There were no differences in tiller length between any pulsed treatment and the controls in *Bromus, Taeniatherum* or *Agropyron* (repeated measures pulse x time interaction $P=0.43$ *Bromus*, $P=0.38$ *Taeniatherum*, $P=.38$ *Agropyron*, Fig. 11A,B,D). *Pseudoroegneria* did increase tiller height in response to the early- and midspring pulses, but not in response to the late-spring pulse relative to controls (pulse x time interaction $P=0.14$, Fig. 10C). *Artemisia* twig lengths were greater in the pulsed than in the control treatment (pulse x time interaction $P=0.15$, Fig. 10E). However, increases in *Artemisia* twig lengths occurred prior to pulse application in the mid- and late-spring treatments, which call the significance of these differences into question. As with the root growth patterns, *Chrysothamnus* did not respond differently to any of the nutrient treatments (pulse x time interaction $P=0.50$, Fig. 10F).

New tiller production by the grass species was generally stimulated by N pulses

that occurred during their early growth phases (Fig. 11, see Tables 2-5 in Appendix 2). *Agropyron* initiated more tillers than any other species as a result of the early and midspring pulses (P=0.0011). *Bromus* increased tiller production in the early and midspring (P=0.085), while *Taeniatherum* increased tiller production as a result of mid- and late-spring pulses (P=0.016). However, in both the annual grasses, the second pulse stimulated a flush of new tillers, which did not reach maturity prior to plant senescence. *Pseudoroegneria* did not respond with increased tiller production to any of the N pulse treatments (P=0.28).

Plant biomass was strongly affected by treatments. Continuous N supply usually resulted in less biomass than did pulses of N. Nearly all species responded to at least one pulse with greater shoot biomass and, in some cases with greater root biomass, than in the control (Fig. 12, see Tables 2-7 in Appendix 2). All grasses increased shoot mass in response to pulsed N treatments (P=0.10 *Bromus*, P=0.0031 *Taeniatherum*, P=0.0017 *Pseudoroegneria*, P=0.024 *Agropyron*, Fig. 12A-D); the greatest treatment effect generally occurred during early growth. Shoot biomass was greatest as a result of the early-spring pulse in *Bromus*, *Pseudoroegneria,* and *Agropyron*, while *Taeniatherum* biomass was greatest as a result of the mid- and late-spring pulses. In contrast to the rather consistent shoot responses, only *Taeniatherum* and *Agropyron* root biomass production was affected by N-pulses ($P \leq 0.05$, both species). These root responses occurred as a result of the same pulses as the shoot responses, with highest root biomass in the early spring for *Agropyron* and in the mid- and late-spring pulse for *Taeneatherum*.

The very long growing season of the shrub species means that the pulses represented proportionately less of the overall N budget than for the other growth forms due to continued background fertilization throughout the experiment. Therefore, differences in final biomass were more difficult to detect. *Artemisia* shoot and root biomass responses were less pronounced than that of the grasses, but still evident. However, unlike the grasses, root (P=0.13) and shoot (P=0.13) biomass responses were not parallel. *Artemisia* root biomass was greatest as a result of the early-spring pulse, while shoot biomass was greatest as a result of the midspring pulse. As with all the grass species, plants receiving the continuous N supply had the lowest shoot and root biomass. In contrast to the marked biomass differences in response to pulses and controls in the other five species, there was no evidence of a shoot (P=0.46) or root (P=0.92) response to any of the treatments by *Chrysothamnus*.

DISCUSSION

Plants grown under the control continuous N supply consistently had lower growth rates, fewer tillers, and less biomass production than plants that received N in pulses. The exception to this pattern is *Chrysothamnus*, which was indifferent and responded to all pulses and the control N supply with equivalent growth rates and biomass production. While pulses generally resulted in greater biomass production than controls, no one pulse resulted in the greatest response in all species, as each species responded differently to the set of pulses. Instead of benefitting from a season-long continuous supply of N, there

were times during the growing season where plants were apparently at the appropriate phenological stage to be capable of very effective uptake of N-rich pulses and were able to use the N for significant gains in biomass production.

Our findings generally correspond with laboratory studies that examined the performance of plants growing under pulsed and continuous supply. However, lower growth of control plants may have been largely due to a lower total quantity of nutrient supply (Crick and Grime 1987, Benner and Bazzaz 1988, Campbell and Grime 1989, Miao and Bazzaz 1990), since none of these studies used equivalent amounts of N in the pulses and continuous delivery. Our comparison of pulsed and continuous N deliveries using equal quantities of N is a unique test of the performance of mature field-grown plants growing under these contrasting patterns of N supply.

In our study, plant phenological stage was very important in determining whether plants responded to the different pulses. The greatest growth response to pulses occurred early in the vegetative growth phase of each species when relative growth rates were highest. In a comparison of six old-field species, McKane et al. (1990) also found a strong phenological component in species responses to seasonal timing of N availability. For all six species they studied, N uptake was greatest in early phenological stages. In contrast, Jonasson and Chapin (1991) found no evidence of phenological effects on responses to pulses of phosphorus by the perennial tussock grass, *Eriophorum vaginatum*. Results from laboratory studies are also inconsistent. Benner and Bazzaz (1988) described greater biomass from early than from later pulses by two annual plant species, *Abutilon*

theophrasti and *Datura stramonium*, whereas Miao and Bazzaz (1990) reported greater biomass in two species of *Plantago* from later than earlier pulses. Thus, while the importance of early growth phases in our experiment is clear, this pattern may not hold in other cases. The timing of plant growth responses was not affected by pulses, even though the magnitude of growth was. For example, the early-spring pulse did not result in an immediate increase in root or shoot growth by *Pseudoroegneria*, but rather more growth during the period of maximum seasonal growth rates. These delayed growth responses by *Agropyron* and *Pseudoroegneria* to the early spring pulse suggest uptake and storage of N. Pulses also resulted in subtle changes in grass, but not in shrub phenology. The early spring pulse stimulated earlier production of flowering tillers, while the late spring pulse delayed senescence. Thus, plant phenological stage at the time a pulse was perceived was crucial in determining plant response, and in turn, pulses had some effect on phenology of the grasses.

The greater capacity of *Agropyron* than *Pseudoroegneria* to capture N from pulses relative to controls is indicated by proportionately greater increases in biomass relative to controls (100% vs 50% maximum increase in the early spring), and may be attributed to differences in both phenology and morphology. *Agropyron* roots grow earlier in the spring than *Pseudoroegneria* and remain active later into the summer (Thorgeirsson 1985, Eissenstat and Caldwell 1988a,b). In addition, *Agropyron* roots have substantially greater root length per mass (specific root length, SRL) than *Pseudoroegneria* (Caldwell and Richards 1986), and therefore, greater absorptive surface areas and potentially greater

capacity for N uptake. The morphological plasticity exhibited by *Agropyron* in its ability to produce new tillers in the spring greatly enhanced the capacity of *Agropyron* to increase shoot biomass. In contrast, once *Pseudoroegneria* had produced a cohort of tillers in the early spring, it did not have the capacity for subsequent new tiller production and increased biomass could only occur through increasing tiller size.

Because of the asynchrony in the timing of *Artemisia* root and shoot growth (Fernandez and Caldwell 1975), final root biomass production was greatest following the early-spring pulse whereas final shoot biomass was greatest following the midspring pulse. Interestingly, root growth following the early-spring pulse did not translate into increased shoot biomass. Therefore, root:shoot ratios were greater as a result of the early-spring pulse, and lower as a result of the midspring pulse. These results suggest that during active growth, N was not stored, but instead contributed to the biomass of the structures with the greatest current demand and, secondly, the temporal pattern of N availability may affect the relative contribution to root and shoot biomass.

In contrast to the other species, there is little evidence in this study that *Chrysothamnus* responded to any of the pulses. There were no significant differences in root or twig growth rates nor in biomass production as a result of pulses relative to the continuous N supply. However, increased leaf N concentrations indicated that *Chrysothamnus* was able to capture some of the N from the mid- and late-spring pulses. In addition, phenological stage does not explain this lack of reaction as *Chrysothamnus* had produced in excess of half its annual shoot biomass increment by the time of the third

pulse and therefore was actively growing during at least one pulse. *Chrysothamnus* is vigorous in its natural setting with high growth rates and pronounced responses to nutrient availability (Davis et al. 1985, Donovan and Ehleringer 1994, Donovan, pers. comm.). Therefore, there is no fundamental reason to suggest that *Chrysothamnus* is incapable of coping with fluctuating nutrient availability. An alternative explanation is that *Chrysothamnus* was very responsive to fluctuating N supply, and maintained equivalent productivity regardless of N supply regime. Because of the high variability among *Chrysothamnus* individuals and small sample size, the power to detect treatment differences in *Chrysothamnus* was low. Therefore, the lack of treatment differences must be viewed with caution.

The annual grasses, *Bromus* and *Taeniatherum*, both reacted to two of the pulses with greater biomass production than controls. However, only the pulse applied during vegetative growth increased the number of tillers that matured and produced seeds. *Taeniatherum* responded later in the season than *Bromus*. In addition, because of their short growing season, *Bromus* and *Taeniatherum* had more constrained windows of opportunity for acquiring nutrient pulses than the perennial species. This means that both species missed one of the pulses and some of the control N supply. However, these plants were growing for 80-90% of the time the control N was applied and therefore, lack of control N does not explain these species responses to pulses as compared to controls. The length of the growing period for these annuals varies with the environmental conditions of each growing season (Mack and Pyke 1983), and the size of the window can be expected

to vary from year to year. Thus, the capacity of these annual species to capture nutrient pulses will be strongly dependent on their phenological development in relation to seasonal conditions.

The invasion of the Great Basin system by these annuals has converted many areas from perennial to essentially annual plant communities (Mack 1986, Billings 1994). Although these annual grasses responded strongly to some pulses in the spring, they are not present as active plants after late spring and, therefore, would miss ephemeral nutrient pulses associated with rain in the summer and fall. With the onset of rainy weather following summer drought, leaching from litter, microbial lysis, and stimulated mineralization may result in significant fall pulses of nutrients. Thus, nutrients that would normally be retained in a system dominated by perennials would be lost from an annual plant community.

The early-spring pulse, a predictable natural pulse in this ecosystem, resulted in the greatest biomass production by *Bromus*, *Agropyron*, and *Pseudoroegneria* and the greatest root biomass production by *Artemisia*. This suggests that the cold-season adapted species of the Great Basin system are well-suited to take advantage of predictable early-spring pulses. In addition, the combination of rapid growth rates and favorable early spring growing conditions also suggests that there is little temporal differentiation in maximum N uptake capacity between these species and therefore, competition for limiting nutrients may be intensified during this time. In contrast, the deeper roots and later phenological development of *Chrysothamnus* result in a much later period of major

activity than for the early-season species. Our results suggest a pattern in the Great Basin where a majority of plant species are cold-season adapted and grow under competitive conditions and where others, such as *Chrysothamnus*, largely avoid competitive conditions by growing when other species are sensecent or quiescent. In contrast to our study, which shows little evidence for temporal niche separation by the majority of species, McKane et al. (1990) found temporal differences in N uptake between competitive dominants in an old field where plant growth is not limited by the onset of summer drought. In the Great Basin, plants are subjected to periods of high moisture and nutrient availability, followed by drought conditions where characteristics of tolerance and avoidance become important. During optimal growing conditions, plants respond effectively to pulsed nutrients and competition is probably intensified by short-term pulse phenomena. Thus, plants must not only be good competitors, but they must also be able to persist during drought conditions.

The capacity for plants to utilize pulses of N in excess of continuously supplied controls strongly supports the importance of pulsed nutrients as a potential resource for plants. The timing of a pulsed resource is crucial in determining its effect on plant growth. Although all pulses increased productivity for at least one species, pulses occurring in the early spring resulted in the greatest response by the greatest number of species. Responses to pulse timing was species-specific. Maximum responses occurred in early vegetative growth stages when growth rates were high. Thus, pulses are important nutrient resources for plants, and the capacity for a plant to respond to any one pulse is dependent upon the phenological stage of the plant.

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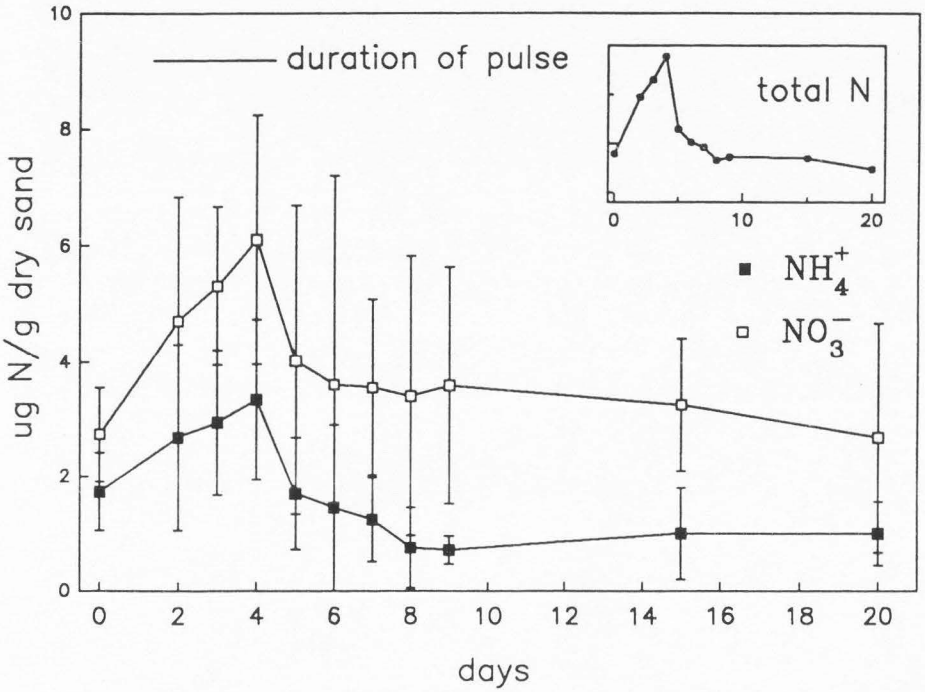

Fig. 6. Sand N content during and following a four-day midspring N pulse delivered as NH_4NO_3. Values represent 2 M KCl sand extracts expressed as NH_4^- and NO_3^+ or total inorganic N (inset). Each data point represents the mean from six species and four replicates (n=24). Analysis of variance indicated no statistical differences in soil N content based either on species or on timing of pulse. Error bars are one standard error from the mean.

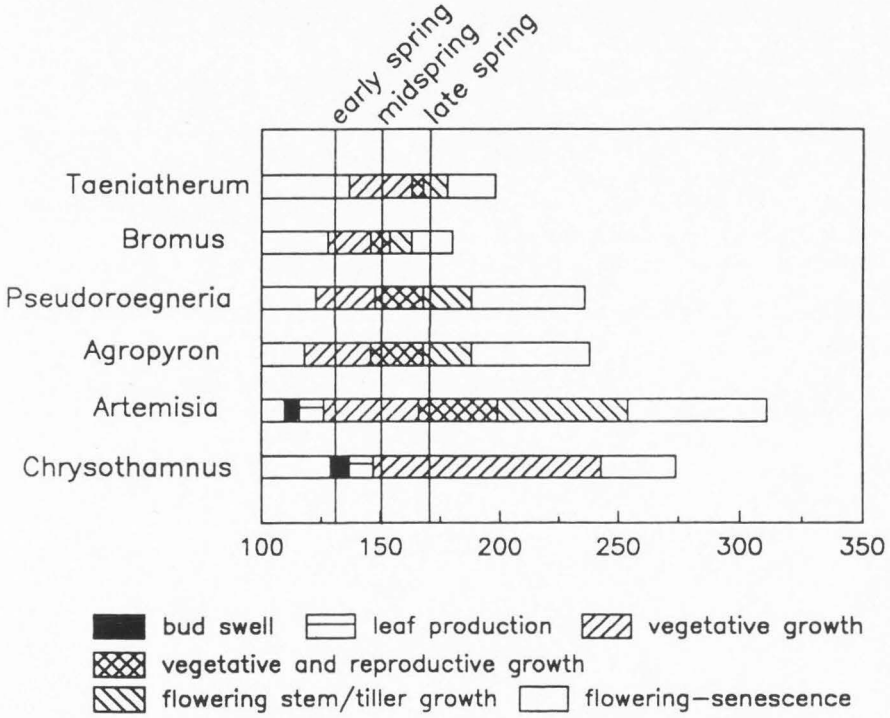

Fig. 7. Plant phenological progression for each of six study species by Julian date. Phenological stage is shown by bar type. Phenological information was collected weekly on experimental plants. Vertical lines indicate the time of each pulse application.

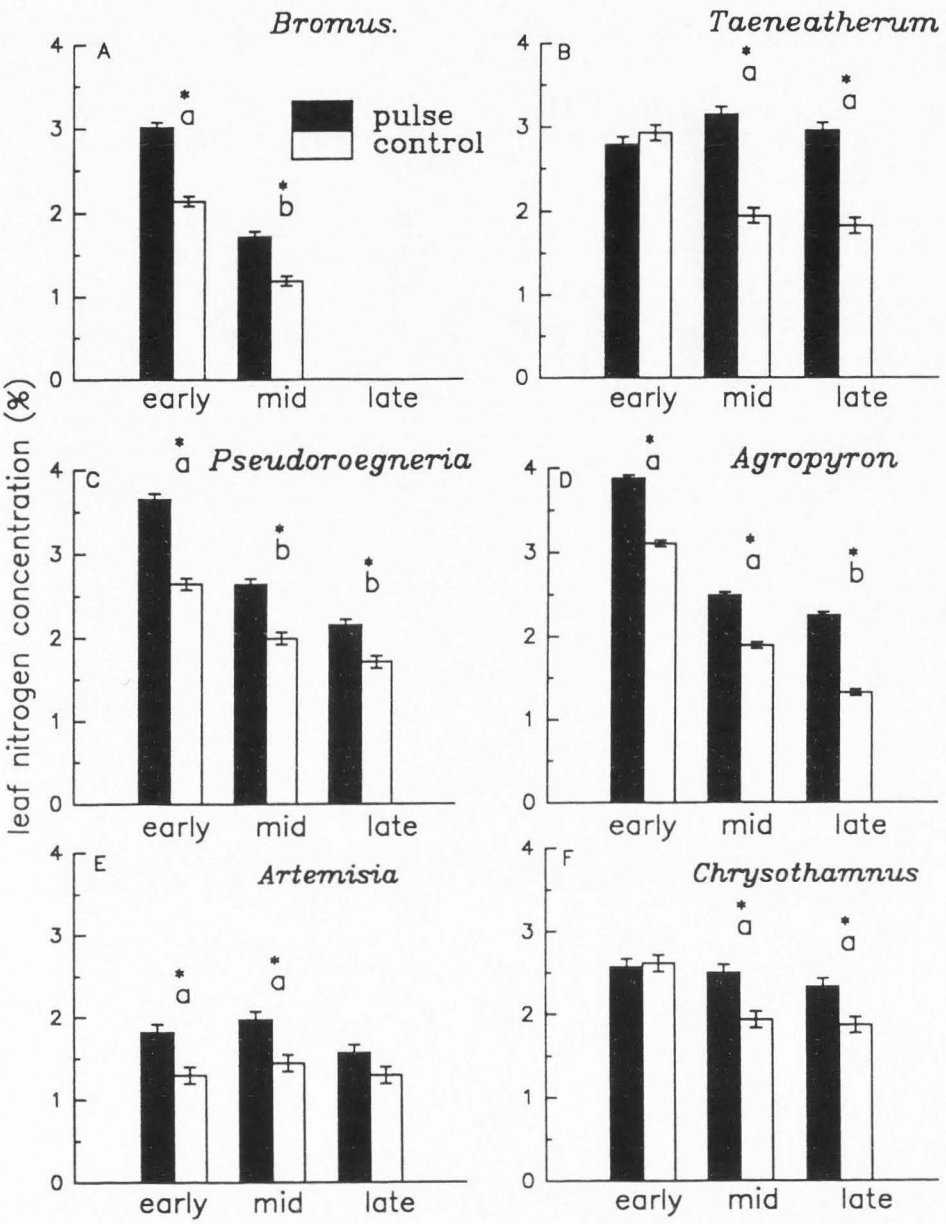

Fig. 8. Leaf N concentration for pulsed and control plants for each species. Leaf samples were collected from control plants (open bars) and plants receiving pulses (solid bars) ten days after the initiation of each pulse treatment. Asterisks indicate significant differences between the pulse and control ($P<0.05$) for individual pulse treatments. Small case letters indicate significant differences in the magnitude of response (pulse minus control) between pulse treatments. Values are mean and standard error for a sample size of four.

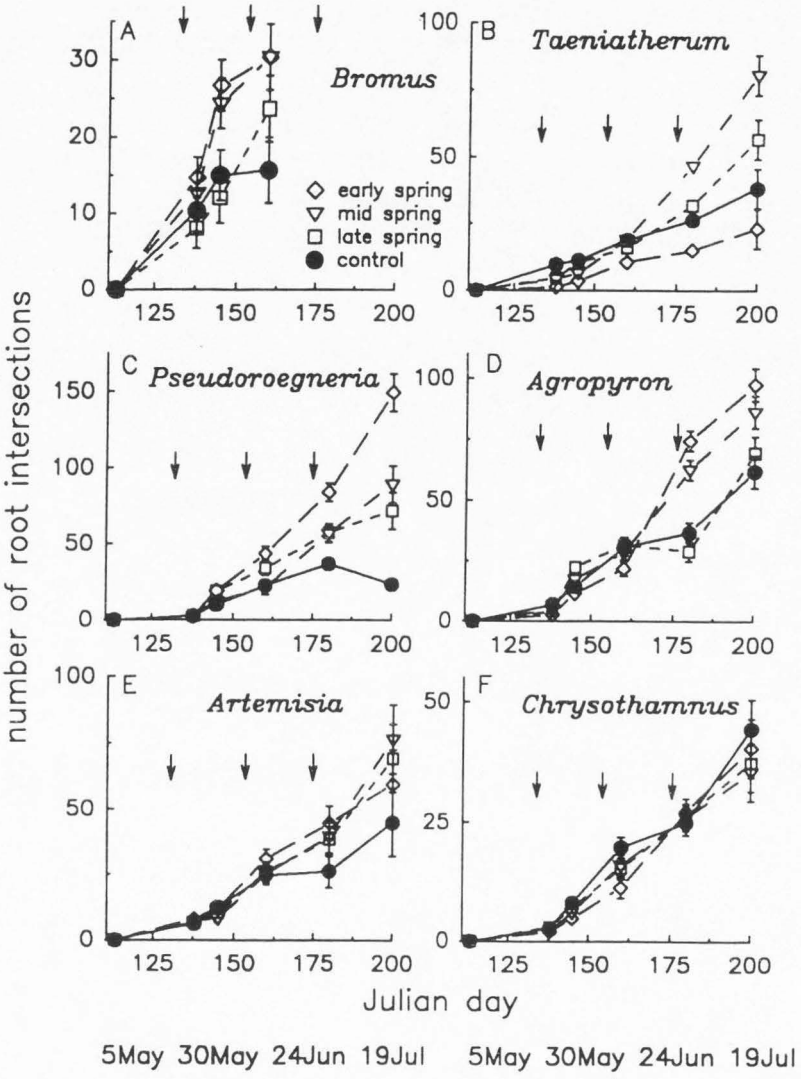

Fig. 9. New root production expressed as the sum of the number of new roots intersecting lines at 5 cm intervals from 5-50 cm depth along minirhizotron tubes by Julian date. Graphs A-F are each of the six study species (as labelled). Each graph contains root intersections from the three pulses (open symbols) and control plots (closed symbols). Values are mean and standard error for a sample size of four. Note different y-axis values for each species.

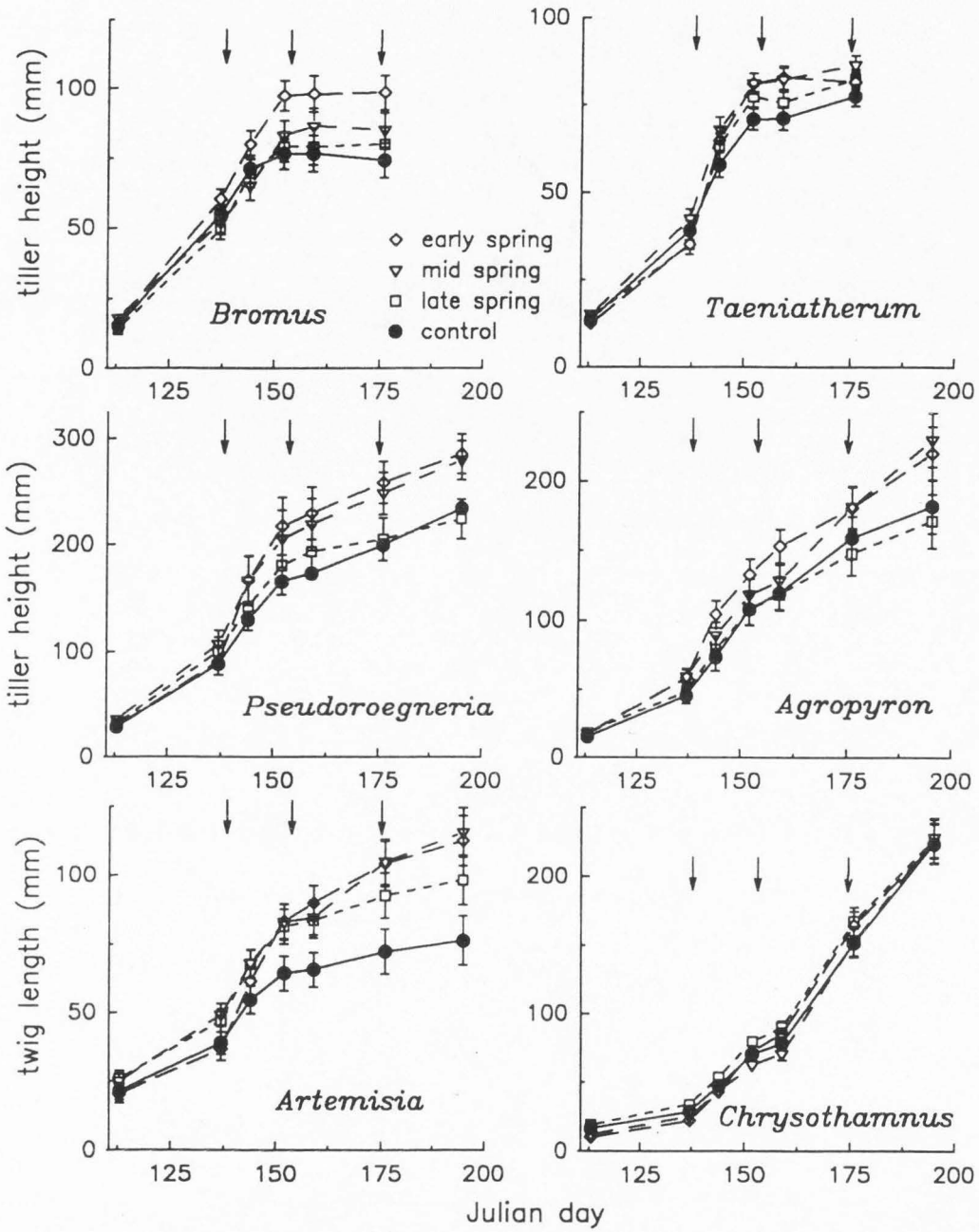

Fig. 10. New shoot growth expressed as tiller length (grasses) or twig length (shrubs) by Julian day. Graphs A-F are each of the six study species (as labelled). Each graph contains mean length and standard error from a sample size of four for each of the three pulses (open symbols) and control (closed symbols) plants. Note different y-axis scales for each species.

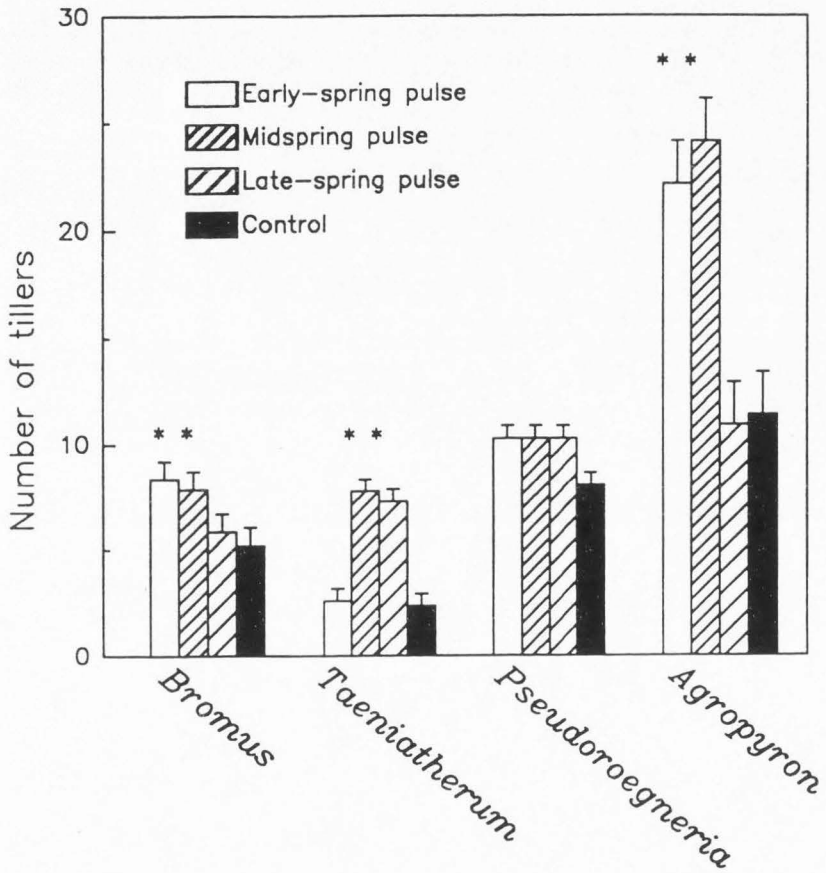

Fig. 11. Number of tillers produced by each grass species for each pulse. Values represent the mean and standard error from four replicates. Significant differences between each pulse treatment and the control treatment are indicated by asterisks ($P<0.05$).

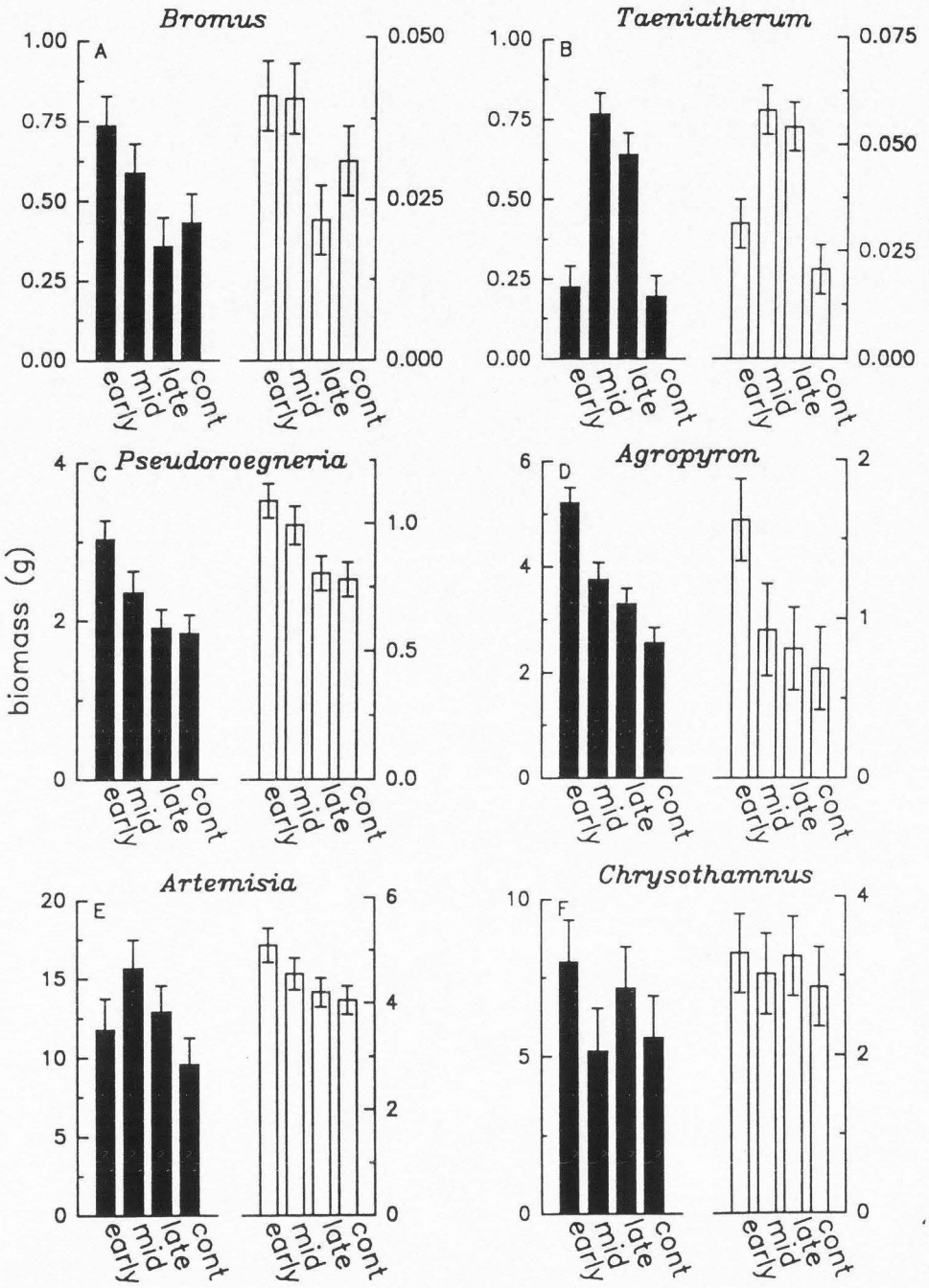

Fig. 12. Shoot (solid bars) and root (open bars) biomass production for each species (A-F, as labelled) for pulsed and control plants. Values are mean and standard error for a sample size of four. Note different scales along y-axis for each species.

CHAPTER IV

THE ROLE OF ROOT BIOMASS AND ROOT UPTAKE CAPACITY IN EXPLOITATION OF N PULSES BY FOUR GREAT BASIN SPECIES

ABSTRACT

In a previous study, we studied the growth responses of Great Basin plant species to short-term pulses of nitrogen (N) that were applied at three different times of the spring growing season. We found that these species were very effective in exploiting pulses of N, and that this ability changed with the phenological stage of the plant. In this study, we repeated the same three pulse treatments, and measured root biomass at the time of each pulse, specific root length (SRL), and root uptake capacity of excised roots before and after pulses. Despite considerable temperature differences and changes in plant phenological stages, root uptake capacity remained remarkably constant for all four species throughout the season. This consistency of root uptake capacity indicated that uptake capacity did not explain the marked seasonal differences in biomass production that occurred in the previous study. In addition, all four species downregulated uptake capacity in the early spring following a pulse, and upregulated uptake capacity in the late spring following a pulse. The SRL decreased throughout the spring, while root biomass increased throughout the season. Because biomass production in response to pulses declined through the season, root biomass does not explain these responses. Instead, we suggest that the quantity of actively growing fine roots, plus the ability to effectively

exploit the soil volume in the early spring, results in capture of a large number of nutrient pulses.

INTRODUCTION

Plants are continually exposed to an environment in flux. As part of growth, survival, and reproduction, plants must effectively utilize resources that vary in availability over time, on both a seasonal basis and within seasons. Nutrients and water become available in ephemeral pulses, and these pulses may be important nutrient sources for plants (Campbell and Grime, 1989; Chapin, Schulze, and Mooney, 1990; Jonasson and Chapin, 1991). Differences in plant species' ability to detect and exploit these temporally heterogeneous resources may determine the competitive hierarchy of a plant community, and thus be an important factor in community structure and function. In a previous study (Bilbrough and Caldwell, in press), we examined the growth responses of six Great Basin plant species to pulses of nitrogen (N) that were applied at different times of the spring growing season. Although the ability to respond to pulses was different for each species, most species were effective in exploiting pulses of N. All but one species produced the greatest biomass in response to a pulse of N that occurred during early phenological stages when plant growth rates and demand were high. Because most of these species are adapted to grow in the cold, early spring, this maximum response generally occurred in the early spring. The exception to this pattern was *Chrysothamnus nauseosus,* which responded equally to all N treatments. Surprisingly, when the same quantity of N was

supplied continuously rather than in a single pulse, most of the species had lower growth rates and less biomass production than plants receiving the N in pulses. Thus, the ability of these species to acquire N supplied in pulses varied during the spring, and was related to plant phenological stage.

Plant exploitation of pulses is determined by the amount of actively absorbing root surface area and the physiological uptake capacity of these roots, plus any changes in root characteristics that may occur as a result of a pulse. Nutrient pulses may stimulate root uptake capacity and also result in increases in root absorptive surface area through root proliferation. However, the enhanced nutrient capture realized through root growth responses may be too slow to be effective in exploiting a pulse. There was no indication from root growth measurements in our prior study that root proliferation had occurred following a pulse (Bilbrough and Caldwell, in press). Under these circumstances, the most likely root system response to a nutrient pulse would be changes in physiological uptake capacity. When nutrients were supplied in localized pulses, the perennial tussock grasses *Agropyron desertorum* and *Pseudoroegneria spicata*, and the woody shrub *Artemisia tridentata* elevated their uptake capacities relative to roots from localized water pulses (Jackson, Manwaring, and Caldwell, 1990). However, the strength and timing of their responses varied among the species (Jackson, Manwaring, and Caldwell, 1990). These changes in root uptake capacity might also take place when the entire root system is exposed to a pulse of abundant nutrients, but this might differ among species.

Plant characteristics that contribute to their ability to exploit nutrients from pulses are

likely to change considerably during the growing season. Root biomass and, therefore, root surface area increase with plant size, and plant nutrient demand changes with phenological stage, growth rate, and the nutritional status of the plant. These changes in demand and the general availability of photosynthate may result in differences in root physiological uptake capacity. Plants take up most of their N, and have their highest growth rates in their early growth stages (Caldwell et al., 1981; Shaver, Chapin, and Gartner, 1986), which may result in high nutrient demand. When plants of the same growth stage were compared, field-grown *Agropyron desertorum* plants that were fertilized with N had lower uptake capacities than plants that had not been fertilized (BassiriRad, Caldwell, and Bilbrough, 1993). This is also known from studies with several species grown in solution culture (e.g. Lee and Drew, 1986; Lee and Rudge, 1986; Hole et al., 1990). Thus, the variable responses of plants that we detected to pulses of N over the spring growing season may reflect changing plant demand for nutrients as determined by phenology and nutrient status.

Abiotic factors such as soil temperature also affect the ability of plants to respond to nutrient pulses. Soil temperature has a direct effect on root growth rates and physiological uptake processes of both NO_3^- and NH_4^+ (Macduff, Hopper, and Wild, 1987). Many Great Basin plant species are adapted to grow during the early spring when snow melt and spring rains have recharged the soil moisture (Dobrowolsky, Caldwell, and Richards, 1990). In the Great Basin, soil temperatures increase from about 5°C at the beginning of the growing season to as high as 27°C by the end of the growing season,

when plant growth becomes increasingly limited by low soil moisture. However, the maximum growth rates and the greatest response to pulses occurred at low soil temperatures when soils were still moist (Bilbrough and Caldwell, in press). Therefore, the plant properties that allowed these plants to exploit pulses of N were effective at low soil temperatures.

In this study, we repeated the same pattern of pulses in order to determine which root characteristics were important in shaping the responses of these species to pulses at different times of the season. We measured root uptake capacity using excised roots before and following pulses to determine both the capacity of the plants at the time of the pulse as well as the effect of pulses on root uptake capacity. We also evaluated the potential role of root biomass and specific root length (the ratio of root length:root mass, SRL) in the exploitation of N pulses. Because of the lack of evidence for proliferation during the course of a single pulse in the earlier study (Bilbrough and Caldwell, in press), we focused our efforts on measuring the status of the root system at the time pulses occurred, and on changes in uptake capacity in order to see how these patterns changed over the growing season and in response to the individual pulses. In many arid ecosystems, NO_3^- is the predominant form of N available to plants (West, 1991). However, recent studies conducted in the Great Basin (Jackson and Caldwell, 1993; Ryel, Caldwell, and Manwaring, in press) indicate that NH_4^+ can also be prevalent in this ecosystem. Accordingly, N pulses were applied in the form of NH_4NO_3. To address the question of the role of uptake capacity in determining the plant responses to pulses we measured in

the earlier study, it was necessary to use the same form of N in our root uptake capacity measurements. Therefore, root uptake capacity represents the sum of NH_4^+ and NO_3^- uptake, rather than single-ion uptake kinetics, and should reflect the role of uptake capacity in the ability of plants to capture these pulses of N.

We studied four species, two woody shrubs and two perennial tussock grasses that commonly co-occur throughout the Great Basin. The woody shrubs *Artemisia tridentata*, ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) and Chrysothamnus nauseosus (Pallas) Britt. (rubber rabbitbrush) are ubiquitous and increase substantially in disturbed systems. The native perennial tussock grass *Pseudoroegneria spicata* (Pursh) Löve (bluebunch wheatgrass) is intolerant of the heavy grazing by cattle and sheep that has occurred in this system (Caldwell et al., 1981). Areas where *Pseudoroegneria* has declined are commonly rehabilitated with the more competitive and grazing tolerant species, *Agropyron desertorum* (Fish. ex. Link) Schult. (crested wheatgrass), a perennial tussock grass introduced from Eurasia.

MATERIALS and METHODS

This study was conducted in the spring of 1994 at the Utah State University Green Canyon Research Area, located 4 km northeast of Logan, Utah (41°45'N, 111°48'W, 1460 m elev.). Mean annual precipitation is 468 mm, with much of the precipitation falling as snow in the winter. Mean annual temperature is 8°C. The 1994 spring growing season began in early March and continued into early July. The species used in this study are

adapted to basic soils and conditions of low phosphorus availability due to the calcareous nature of the soils. In addition, N limitation has been demonstrated by N fertilization studies (Bilbrough and Caldwell, 1995; C.J. Bilbrough, Utah State University, unpublished data). More information on the soils of the area is given in Jackson and Caldwell (1991). The site is typical of Great Basin areas where *Artemisia*, *Chrysothamnus,* and *Pseudoroegneria* naturally occur, and where *Agropyron* has been seeded.

The perennial grass species typically initiate growth in the early spring, largely from overwintering tillers, produce reproductive tillers during the midspring, and then enter a dormant state following seed set in the early to midsummer. *Artemisia* is an evergreen shrub. It produces new leaves and vegetative long shoot growth in the early summer. Flowering occurs in the fall and the plant retains foliage over the winter. *Chrysothamnus* overwinters with no leaves and has a prolonged period of bud swell and leaf production prior to long shoot growth in the spring. Vegetative long shoot growth continues throughout the summer with flowers produced on the terminus of the long shoots in the autumn.

Because of the potential for confoundment of a controlled-pulse experiment with the occurrence of natural N pulses, we established 1-m-deep sand-filled plots in the field where root growth was not confined and where nutrient supply could be controlled. Four replicate 5-x-18-m plots were constructed in the spring of 1992, and plants were established in monoculture subplots within each main replicate sand plot the following summer and fall. *Chrysothamnus* and *Artemisia* were planted as 1-year-old seedlings.

The perennial grasses were transplanted from mature tussocks of *Pseudoroegneria* plants from a local population in Green Canyon and of *Agropyron* plants from 13-year-old plots within the Research Area. Additional information on plot design and establishment is provided in Bilbrough and Caldwell (in press). Species were arranged in parallel subplots alternating in growth form, neighboring species and main plot location such that each of the four possible combinations of subplots occurred only once. Thus, rather than randomization of species subplot locations within each main plot, subplots were dispersed with respect to location within the plots and in relation to each other. This was done because of the difficulty in obtaining adequate dispersion with randomization of a small sample size. Combinations of subplots were randomly assigned to the main plots.

As background fertilization, modified low-N Hoaglands solution was applied regularly such that nutrients other than N were applied at one quarter strength of normal Hoaglands solution and at an approximate rate of 2.3 l m^{-2}. Nitrogen was added as 1.0 mM N as NH_4NO_3 at a rate of 0.043 g N m^{-2} (0.43 kg ha^{-1}). Plots were watered using a drip irrigation system.

Experimental design--This experiment was conducted in the spring of 1994, and the same pulse application treatments used in 1993 were repeated (Bilbrough and Caldwell, submitted). Prior to pulse application, we estimated root biomass, measured fine root SRL and N uptake capacity of excised roots. In order to assess the effect of pulses on root uptake rates, we repeated N uptake and SRL measurements seven days following the first day of each pulse. We measured total N uptake of NH_4NO_3, rather than

a single form of N, because this was the form of N delivered to the plants in the field, and our intent was to explain the growth responses detected in 1993 using these forms of N. Therefore, these measurements do not represent single-ion uptake kinetics, rather the summed uptake capacity of both NH_4^+ and NO_3^-.

Each monoculture subplot was divided into four treatment plots consisting of 72 plants arranged in an equally spaced array 12 plants long by 6 rows wide. In the 1993 experiment, treatment plots were randomly assigned to one of four N addition treatments: a control continuous N supply, and three pulses applied during different times of the growing season (early, mid and late spring). All four treatments received the same quantity of N, either applied in one of three 4-day pulses or over a 10-week period (control). We repeated these treatments in the same design in 1994. Therefore, this experiment represents the cumulative response from a pulse applied once a year for 2 years at the same time of the season.

Because of the inherent differences in plant sizes among the species, it was not possible to apply the same quantity of N to all four species. Within a growth form, the same quantities were used. Each pulse was delivered once daily for four consecutive days in the same concentration for all species (3.6 mM N as NH_4NO_3), and with the same volume for each of the two growth forms. Shrubs and grasses received total N applications of 1.95 and 2.0 g N m^{-2}, respectively, over the course of the 4-day pulse (corresponding to 0.093 and 0.063 g N per plant). This was followed by a heavy watering treatment to flush the N below the major root zone. The solution concentration in the

control treatment was 1.4 mM N as NH_4NO_3. The initiation of pulses was staggered over 2 days, with two plots started each day. This was because of the time constraints on processing root cores for nutrient uptake, only two plots per species could be processed in 1 day.

Pulses were applied in the early, mid, and late spring at times when plant phenological stages matched those during the pulse applications the previous year. The early-spring pulse was applied April 14-18, when the grasses were in early vegetative growth, *Artemisia* vegetative stems were growing, and *Chrysothamnus* was in bud-swell stage. The midspring pulse was applied May 12-16 when the grasses were flowering, *Artemisia* vegetative and reproductive stems were growing, and *Chrysothamnus* vegetative stems were growing. The late-spring pulse was applied June 14-18, when the grasses were senescing, *Artemisia* reproductive stems were growing, and *Chrysothamnus* vegetative stems were growing.

Measurements--In order to assess the pattern of sand N concentrations over the course of a pulse and to compare N pulses from this experiment to the experiment conducted in 1993, sand N was extracted in subplots receiving the midspring pulse using 2 M KCl every day for 21 days beginning the day before the pulse treatment. In addition, we collected soil samples by coring for sand N analysis and soil moisture measurements at the time roots were collected for N uptake capacity measurements. Samples were shaken for 2 hours and filtered, and the filtrate was analyzed colorimetrically for NH_4^+ and NO_3^- using a flow-injection autoanalyzer (Lachat Instruments, Mequon, WI). Root biomass in

all treatment plots was estimated at the time of each pulse application. Two cores per subplot were collected and roots removed from the sand using a hydropneumatic elutriation root washer (Gillison's Variety Fabrication, MI, USA). Roots were oven-dried at 80°C and weighed. Plant phenology was recorded biweekly and nondestructive estimates of plant biomass were made at the end of the season in order to make comparisons with the experiment conducted in 1993.

Root N uptake capacity measurements--The N uptake capacity by excised roots was measured on treatment plots prior to (control) and 7 days after the initiation of each pulse. Plants in control plots may not have been comparable with plants in prepulse conditions in the pulsed plots because of differences in plant sizes and possibly different tissue N concentrations between the pulsed and control plots (Bilbrough and Caldwell, in press). Therefore, we used prepulse conditions in the pulsed plots as the basis for comparison. Soil cores 15x50 cm were collected from four treatment plots (four species, one replicate) in the early morning and then four more from a different replicate when the first set had been processed. Roots were sieved from the sand, selected if < 1.0 mm in diameter, and then separated into seven random subsamples. We selected narrow diameter roots in order to assay only young, active roots. One subsample was used to measure SRL, three were incubated at a standard temperature of 20°C, and three were incubated at the ambient soil temperature measured 10 cm from the soil surface at the time of each pulse. The early-spring pulsed roots were incubated at 10°C, the midspring at 14°C, and the late spring at 23°C. Root subsamples were equilibrated in a 0.5 mM $CaCl_2$

solution for 30 minutes either at 20°C or ambient temperature, immersed in 50, 500, or 1000 μmol 99%-enriched $^{15}NH_4{}^{15}NO_3$ for 20 minutes, and then rinsed in cold 0.5-mmol $CaCl_2$. Root samples were oven-dried at 80°C, weighed, ground and analyzed for total N and ^{15}N enrichment with continuous flow direct combustion and mass spectrometry using an ANCA 2020 system (Europa Scientific Inc., Cinncinatti, OH, USA) for total N and percent enrichment with ^{15}N. Because SRL was not measured on entire root samples, neither the fraction of fine roots at each sampling time nor the SRL for the root system as a whole was determined.

Analysis--Quantitative comparisons were conducted at the species level, while comparisons among species were qualitative. This is because species subplot locations were not randomized and therefore, the assumption of random sampling for statistical tests may have been violated. Within each species, where randomness, normality, and independence were reasonable assumptions, analysis of variance procedures to test treatment means were performed using general linear models (SAS 1988). Box plots and normal probability plots of residuals were used to assess normality and outliers. Where appropriate, planned comparisons were conducted using Tukey's t test (pairwise comparisons) or Dunnett's test (control vs treatments) as described by Day and Quinn (1989). Statistical power was low in this experiment because of small sample sizes and high variability common to many field experiments. Accordingly, we did not adhere to the traditional standard of statistical significance at $P<0.05$. While this increases the chances of Type I error (concluding treatment differences when there are none), the alternative

error of concluding no treatment effect when there is one (Type II error) is reduced. *P*-values are included, allowing readers to form their own conclusions.

Root biomass, specific root length (SRL), and root tissue N concentrations were analyzed as single factors with three levels (early-, mid-, and late-spring pulse), followed by pairwise comparisons when the overall test yielded a significant *P*-value. Root uptake rates were analyzed using a mixed model (SAS 1988) in a split-split plot design. Pulse treatment (early, mid, or late spring) was the main plot, prepulse and postpulse were the first split, and laboratory solution concentrations (50, 500, 1000 μmol NH_4NO_3) and temperatures (ambient, 20°C) were the second split.

RESULTS

Root uptake measurements--The patterns of net root uptake capacity immediately before and after a pulse, and over the season were striking in their consistency among species. Root uptake capacity measurements at ambient temperatures demonstrate uptake potential at the soil temperatures plants experience as the growing season progresses and soils gradually warm. Net root uptake capacity measured at ambient temperatures, averaged for prepulse and postpulse conditions and across solution assay concentrations, were not significantly different among pulses for any of the species (Figs. 13-16, P=0.64 *Agropyron*, P=0.25 *Pseudoroegneria*, P=0.30 *Artemisia*, P=0.49 *Chrysothamnus*). Thus, even though considerable differences existed in soil temperatures, root uptake capacity was not different over the course of the growing season for any of the four species

examined (see Tables 8-11 in Appendix 2). When assay nutrient solution concentrations were considered individually, prepulse uptake capacities of *Pseudoroegneria* in the early spring were significantly higher than those later in the season at all solution concentrations (Fig. 14). There is little evidence to suggest differences in uptake capacity by *Agropyron*, *Artemisia*, or *Chrysothamnus* during the season over a wide range of solution concentrations.

The most striking pattern of plant responses to pulses was the consistent differences between prepulse and postpulse uptake capacities over the course of the spring for all species. Relative to prepulse uptake capacities, plants had decreased uptake capacity following a pulse in the early spring, while they had elevated their uptake capacity following a pulse in the late spring. The pattern of decreased uptake capacity following the early spring pulse was apparent in all four species (Figs. 13a-16a). At ambient temperatures, *Pseudoroegneria* (P=0.0003), *Artemisia* (P=0.0004), and *Chrysothamnus* (P=0.0019) significantly decreased uptake capacity at one or more solution concentrations relative to uptake capacity before the pulse. This pattern was not as pronounced in *Agropyron* (P=0.10). In contrast, *Agropyron* (P=0.0008), *Artemisia* (P=0.02), and *Chrysothamnus* (P=0.09) all significantly increased their uptake capacity following the late-spring pulse relative to uptake capacity before the pulse, while differences in uptake capacity of *Pseudoroegneria* were not statistically significant (P=0.35, Figs. 13c-16c). Root uptake rates before and after pulses in the midspring were intermediate to the marked responses in the early and late spring (Figs. 13b-16b). All of these patterns were

also reflected in the 20°C assays (Figs. 13-16, insets). Thus, uptake rates before and after pulses changed with the timing of the pulse, and the pattern of response was remarkably consistent among species and assay temperatures for each species.

Uptake capacities by roots assayed at ambient temperatures were surprisingly similar to uptake capacities of roots assayed at the uniform temperature of 20°C (Figs 13-16, insets). In fact, there were no statistically significant differences in net uptake rates between roots incubated at 20°C and at ambient temperatures for either *Artemisia* (P=0.27) or *Pseudoroegneria* (P=0.35). For *Agropyron* and *Chrysothamnus*, net uptake rates were higher when measured at 20° than at ambient temperatures in the early and midspring, when the temperature differences were greater than in the late spring (P=0.08, *Agropyron*, and P=0.001, *Chrysothamnus*). However, these differences are less than would be expected given the magnitude of the temperature differences. Thus, in spite of considerable temperature and phenological differences, root uptake capacity remained remarkably constant throughout the season.

Net root uptake capacities assayed at the 500-μmol concentration and averaged for prepulse and postpulse conditions illustrate species differences and seasonal patterns (Fig. 17). Regardless of assay temperature or pulse timing, *Agropyron* uptake capacity was greater than that of the other species, which were similar in their uptake capacities at ambient temperatures. Net root uptake capacities of total N measured at 20°C for each of the pulses were an indication of changes in root uptake capacity over the course of the spring growing season. At 20°C, *Pseudoroegneria* uptake capacities were higher than that

of the shrub species, particularly earlier in the spring. *Agropyron* uptake capacities were similar in the early and midspring, but declined markedly in the late spring (Fig. 17a, P=0.016), whereas *Pseudoroegneria* net uptake capacities declined as the season progressed (Fig. 17a, P=0.06). In contrast, there was no evidence that root uptake capacity changed over the course of the spring growing season for either *Artemisia* or *Chrysothamnus* (Fig.17a, P=0.91 *Artemisia*, P=0.36 *Chrysothamnus*).

Net uptake rates of both NH_4^+ and NO_3^- are often negatively related to root tissue N concentrations (e.g., Lee and Rudge, 1986). In this study, however, net uptake rates increased with increasing root tissue N concentrations, and the steepness of the relationship and range of tissue N concentrations were different for each species (Fig. 18). Mean root tissue N concentrations were not significantly different between pulses (P=0.19) or between mean prepulse and postpulse measurements for each pulse (P=0.28). However, when paired at the level of individual treatment plots, root tissue N concentrations were generally greater before the early-spring pulse than after (Fig. 19), but was generally less before the pulse than after the pulse in the late spring (Fig. 19). Root tissue N concentrations in the midspring were intermediate to the early and late spring N concentrations, with some positive (pre>post) and some negative (pre<post) changes. These differences in pre- and postpulse tissue N concentrations are consistent with differences in uptake rates, and suggest tissue N concentration may at least partially explain the uptake capacity changes for pulses at different times of the spring.

Root biomass and root length--As expected from the normal course of plant

growth, root biomass increased through the spring growing season (Fig. 20). For all species, early spring root biomass was significantly lower than root biomass at later sampling dates ($P<0.05$, all species). At the sampling depths of 0-50 cm, *Agropyron* and *Artemisia* root biomass increased from the early to midspring, and leveled off from mid- to late spring. *Pseudoroegneria* and *Chrysothamnus* root biomass continued to increase throughout the spring with significantly higher values with each successive sampling date. This spring-season pattern of root biomass production demonstrates that root biomass alone is not sufficient to explain nutrient uptake ability as maximum plant growth responses to pulses occurred early in plant growth, when root biomass was lowest (Bilbrough and Caldwell, in press).

The SRL was measured on fine root subsamples concurrently with each set of uptake rate measurements. Fine root SRL in the early spring was significantly greater than in the mid- or late spring for all species ($P<0.01$, all species, Fig. 21). Thus, on a mass basis, the amount of root length in the fine root portion of all species declined as the growing season progressed. Grass SRL was always higher than shrub SRL at each sampling time, with *Agropyron* mean SRL values at least twice those of the shrubs and one third greater than *Pseudoroegneria*. This pattern is particularly striking in the early spring, where *Agropyron* mean SRL was 140 m/g, as compared to 89, 70, and 53 m/g for *Pseudoroegneria*, *Artemisia*, and *Chrysothamnus*, respectively.

DISCUSSION

Root uptake capacity measurements indicated that all species were capable of exploiting pulses throughout the spring, even under conditions of cold soil temperatures in the early spring or at low nutrient concentrations at any time in the spring. Despite the considerable temperature differences and changes in phenological stages, root uptake capacity for all species remained remarkably constant throughout the season. There were no differences in uptake capacity during the season at ambient temperatures for any of the species. Uptake capacity was similar among the native species *Pseudoroegneria*, *Artemisia*, and *Chrysothamnus*, while the exotic *Agropyron* had nearly twice the uptake capacity of the other three species. Assays at 20°C also gave no indication of differences in uptake capacity between the two shrub species, *Artemisia* and *Chrysothamnus*, and these were somewhat less than that of *Pseudoroegneria*. Again, the uptake capacity of Agropyron was twice that of the other three species. *Agropyron* and *Pseudoroegneria* had higher uptake capacity earlier in the season than later in the spring as indicated by the 20°C assays, while shrub uptake capacities did not change during the spring. The differences in uptake capacity between the 20°C and ambient temperature assays were not as large as would be expected given the magnitude of the temperature differences. For example, if these processes had a Q_{10} of 2.0, uptake capacity would have doubled between 10° and 20° C. *Agropyron* uptake capacity at 10°C was 67% of the uptake capacity of roots assayed at 20°C, while *Pseudoroegneria* uptake capacity was 85% of the roots assayed at 20°C. Thus, all species exhibited strong plasticity under variable conditions and

maintained homeostasis in uptake capacity. Also, the consistency of root uptake capacity throughout the season suggests that uptake capacity did not play a role in the marked differences in exploitation of the different pulses during the season by the plants (Bilbrough and Caldwell, in press).

The striking and unexpected pattern of downregulation in the early spring and upregulation in the late spring between prepulse and postpulse conditions is remarkably consistent for all species. Root tissue N decreased following a pulse in the early spring, most likely because of transport to the shoot system due to high shoot demand. The question remains, however, as to why plant uptake capacity decreased following this pulse even though growth rates and nutrient demand were apparently high. Root and shoot tissue N concentrations did not suggest that plants were oversupplied with N. It is possible that elevated uptake capacity did occur, but substantially before our measurements at the end of the pulse. Also, the relatively small shoot system under cool, early-spring weather conditions may have been limited in its ability to supply the energy necessary to support enhanced uptake capacity, which is considered to be energetically costly. Thus, rather than upregulation, downregulation occurred by the time the early-spring pulse had been exploited. In the late spring, root tissue N increased in the root tissues following the pulse and uptake rates increased. This occurred at a time when growth rates and demand were probably lower than in the early spring (Bilbrough and Caldwell, in press). At this time, the combination of greater foliage area and warmer weather conditions that would favor higher photosynthetic rates may have provided the

roots with more photosynthate, affording the luxury of upregulation during the course of the pulse.

Earlier studies of plant responses to localized pulses (patches) with these same species were largely conducted in the late spring, when soil moisture was low enough to ensure integrity of a nutrient patch (Jackson, Manwaring, and Caldwell, 1990) . These studies also found elevated uptake capacity by *Agropyron*, *Pseudoroegneria*, and *Artemisia*, and no evidence of downregulation (Jackson, Manwaring, and Caldwell, 1990; Jackson and Caldwell 1991), at the same time of the season that we found upregulation. Thus, it is possible that these elevated uptake capacities found in localized nutrient patches are also influenced by seasonality and plant phenology, and may not occur at other times. However, with patches, only a small proportion of the root system was exposed to the greater nutrient concentrations. Thus, plant demand for the nutrients would not be so greatly influenced as by the pulses in our study where the entire root system was exposed to the excess of nutrients. This variable pattern of responses demonstrates that these species are capable of both down- and upregulation of uptake capacity, and the response may depend on seasonal conditions and plant phenological stage.

In our study, there was a pattern of increasing root uptake capacity with increasing root tissue N concentration, regardless of pulse timing. This relationship between root uptake capacity and root N concentrations was not different among pulses, nor was it different before and after pulses. However, the slope of the relationship and the amount of N in the root tissue varied among species. At the same tissue N concentrations,

Agropyron uptake capacity was greater than that of the other three species, while *Pseudoroegneria* was intermediate to the lower uptake capacities of *Chrysothamnus* and *Artemisia*. Maximum shrub root tissue N concentrations were lower than those of the grasses. Other studies have found that root uptake capacity decreases with increasing root tissue N concentration (e.g., Lee and Rudge 1986, Hole et al. 1990). However, most of these studies were comparing plants of the same growth stage that were deficient in N to those in ample supply, rather than comparing seasonal variation in uptake capacity by plants with low to sufficient N supply. Additionally, root tissue N concentrations were considerably lower in our experiments than in other studies that reported decreasing uptake capacity with increasing concentrations.

As the season progressed, root biomass increased, as expected. This increase in root biomass by itself does not explain plant exploitation of nutrient pulses during the spring. In our earlier study (Bilbrough and Caldwell, in press), the maximum pulse exploitation, as manifested by leaf tissue N concentrations and season-long root and shoot biomass production, occurred in the early spring when root biomass was low. Thus, there is not a direct relationship between root biomass and the ability of a plant to capture a pulse of nutrients. Instead, exploitation of pulses may be dependent on the proportion of the root system that is actively taking up nutrients. Because the timing of growth and development varies among many species that coexist in the same environment, conclusions relating root biomass to uptake capacity should be made with the recognition that root biomass in itself is not a direct reflection or indicator of the nutrient capture ability of a

species.

The SRL decreased with progression of the spring, which suggests that there were many thin, actively growing roots the early spring that would contribute to effective exploitation of the soil through high rooting density relative to biomass invested in the root system. This is particularly true of *Agropyron*, which had very high SRL in the early season, and marked shoot and root biomass increases in response to the early-spring pulse the previous year. Changes in SRL over the season may affect interpretation of uptake capacities because differences in root length per root mass suggest that root surface area may also be different. Thus, it is likely that *Agropyron* root surface area per root mass in the early spring was greater than in the late spring and, therefore, higher surface area and uptake capacity combined explain the higher early spring uptake capacities at 20°C as compared to the late spring.

CONCLUSIONS

In this study, our objective was to determine how root system characteristics changed with season and phenological stage, and how these characters influenced plant growth responses to pulses at different times of the spring. Plants responded to all pulses with greater biomass than controls, and this response varied with the phenological stage of the plant. There does not appear to be a simple explanation for these responses. While our measurements of uptake capacity revealed a remarkable ability to maintain homeostasis in uptake rates over a wide range of temperatures and plant phenological

stage, the very consistency of these rates indicates that they cannot explain the marked seasonal differences in biomass production in response to different pulses that were found earlier (Bilbrough and Caldwell, in press). Because root biomass increased during the spring while growth responses to pulses declined through the season, root biomass in itself also cannot explain these differences. The SRL measurements indicate that the young, actively growing roots were finer in the early spring. We suggest that the quantity of actively growing fine roots and the physiological ability of these root systems to rapidly take up N in the early spring despite low soil temperatures result in effective capture of nutrients from these early-season pulses.

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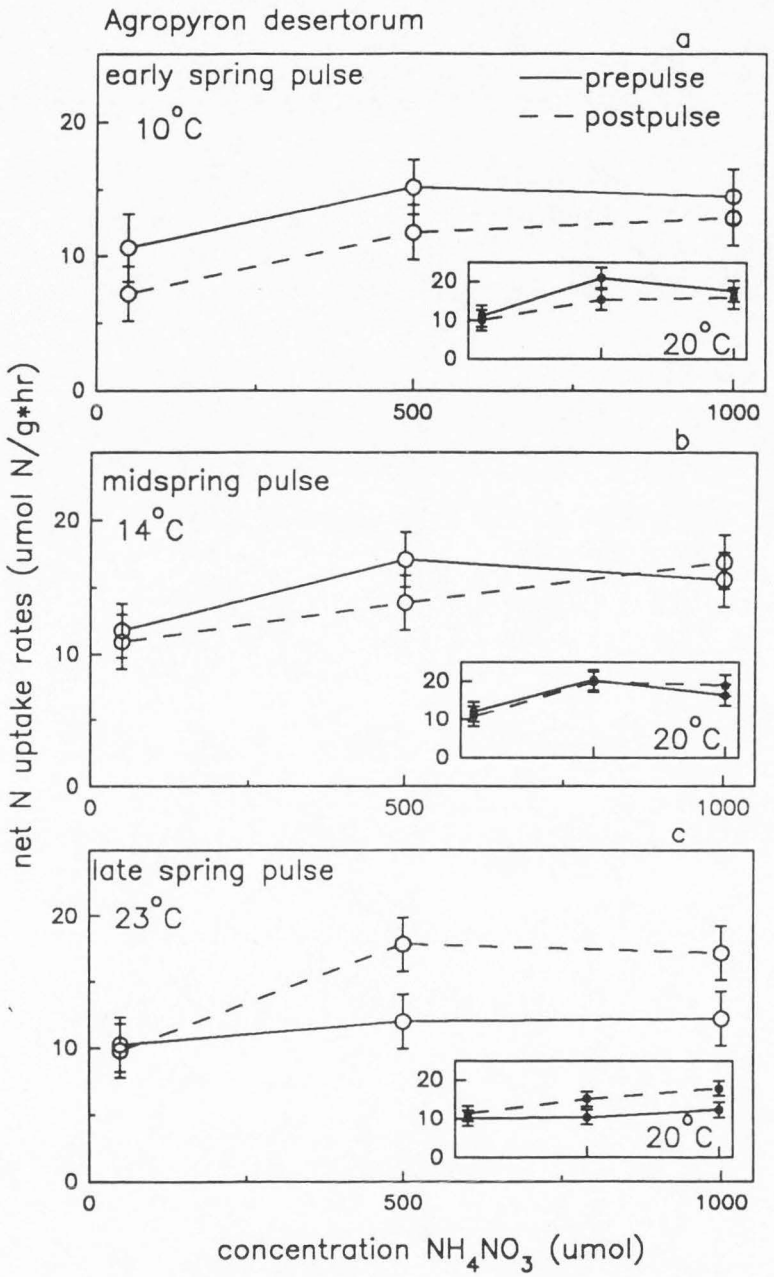

Fig. 13. Net uptake rates of NH_4^+ and NO_3^- combined for *Agropyron desertorum* for the a) early-spring pulse, b) midspring pulse, and c) late-spring pulse. The larger graphs are uptake rates measured at ambient temperatures; the insets are uptake rates measured at 20°C. Each value is a mean with one standard error from a sample size of four.

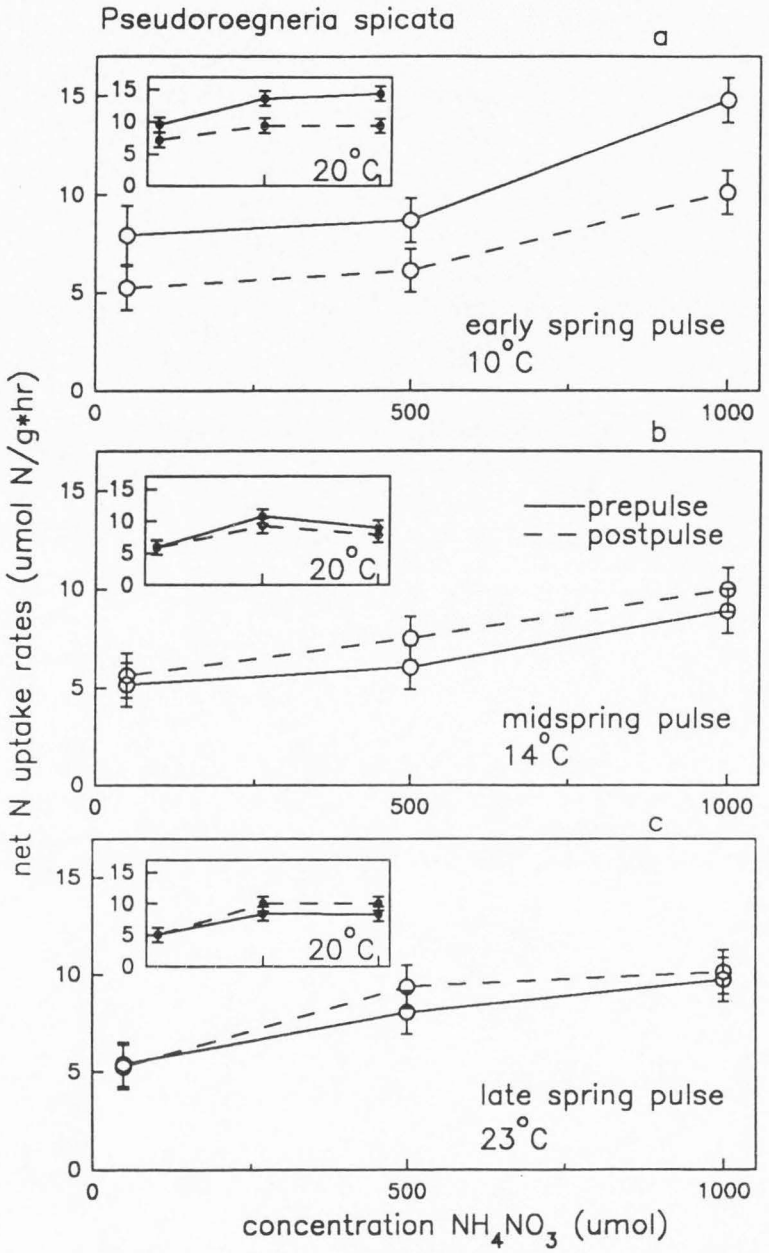

Fig. 14. Net uptake rates of NH_4^+ and NO_3^- combined for *Pseudoroegneria spicata* for the a) early-spring pulse, b) midspring pulse, and c) late-spring pulse. The larger graphs are uptake rates measured at ambient temperatures; the insets are uptake rates measured at 20°C. Each value is a mean with one standard error from a sample size of four.

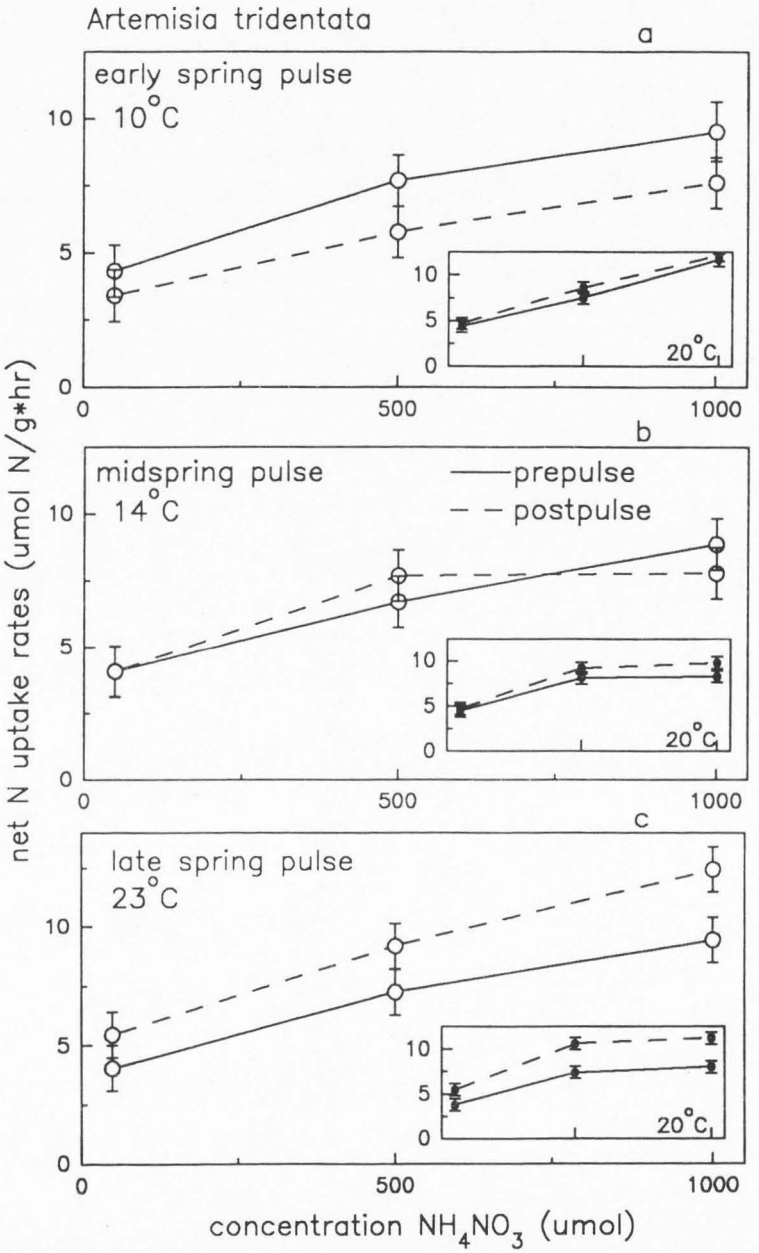

Fig. 15. Net uptake rates of NH_4^+ and NO_3^- combined for *Artemisia tridentata* for the a) early-spring pulse, b) midspring pulse, and c) late-spring pulse. The larger graphs are uptake rates measured at ambient temperatures; the insets are uptake rates measured at 20°C. Each value is a mean with one standard error from a sample size of four.

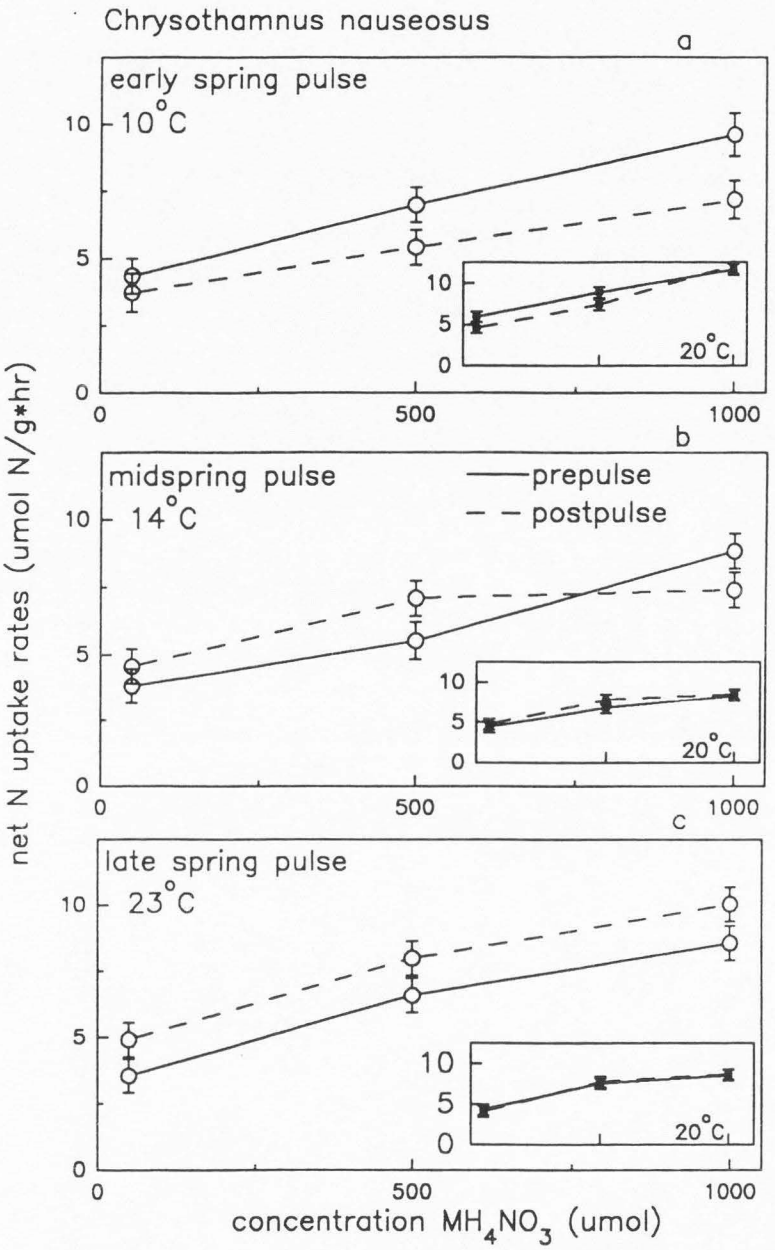

Fig. 16. Net uptake rates of NH_4^+ and NO_3^- combined for *Chrysothamnus nauseosus* for the a) early-spring pulse, b) midspring pulse, and c) late-spring pulse. The larger graphs are uptake rates measured at ambient temperatures; the insets are uptake rates measured at 20°C. Each value is a mean with one standard error from a sample size of four.

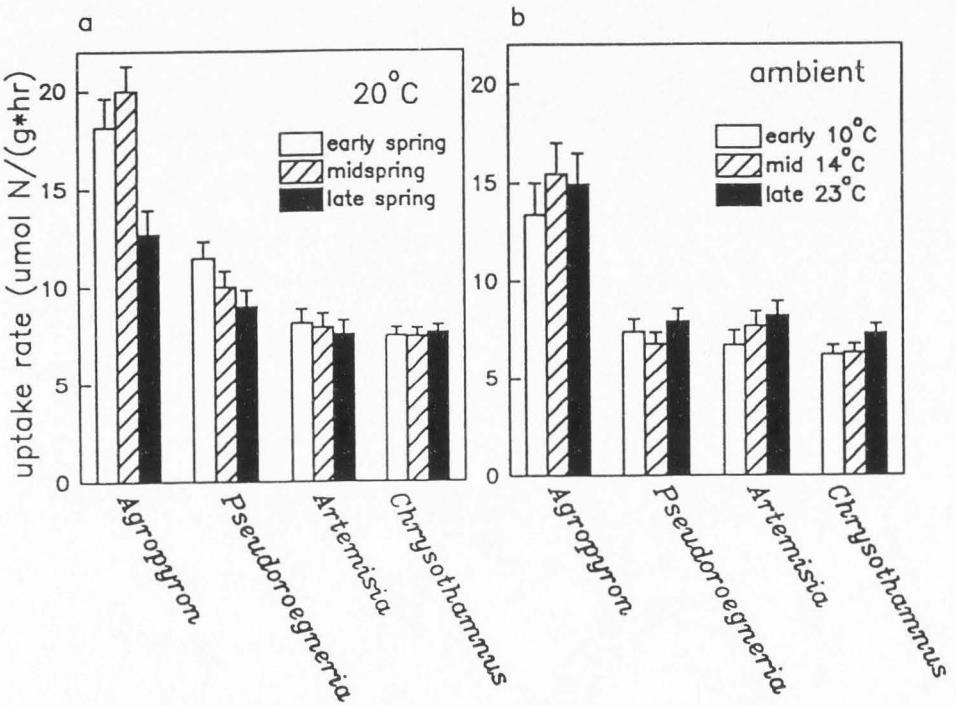

Fig. 17. Mean net uptake rates of NH_4^+ and NO_3^- combined for the early-, mid-, and late-spring pulses for each plant species at a) a uniform temperature of 20°C and b) ambient temperature at the time of each pulse. Means are averaged over prepulse and postpulse measurements and at the 500 μmol concentration. Each bar is the mean plus/minus one standard error from a sample size of 24.

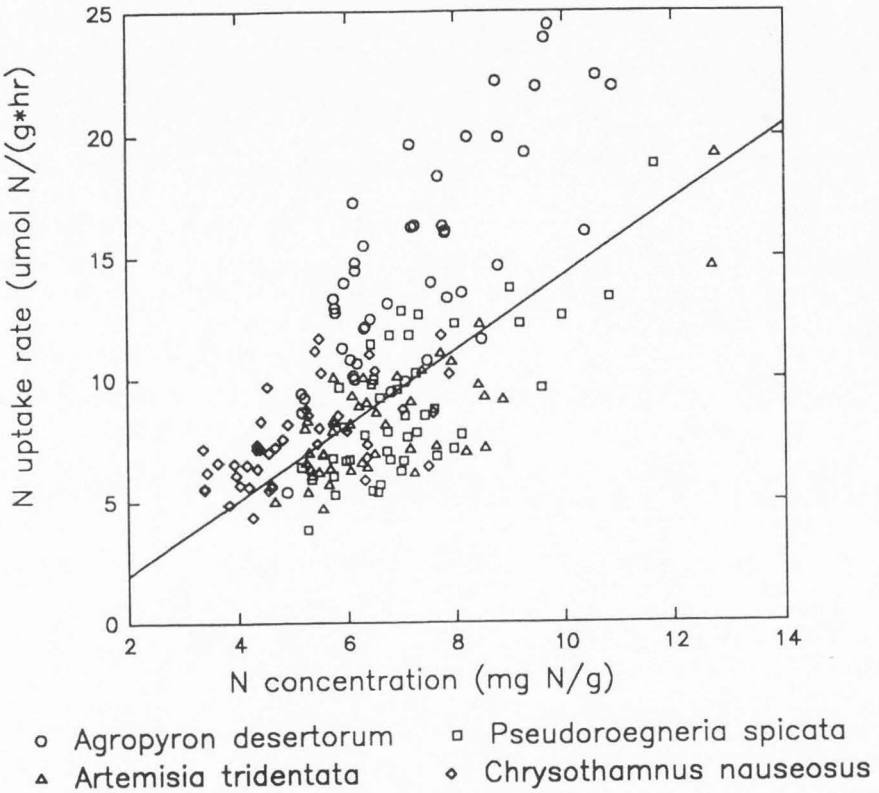

Fig. 18. The relationship between total net N uptake rates and root tissue N concentration. Each value represents an single sample of root, and includes all pulse treatments for pre- and postpulse conditions and all species.

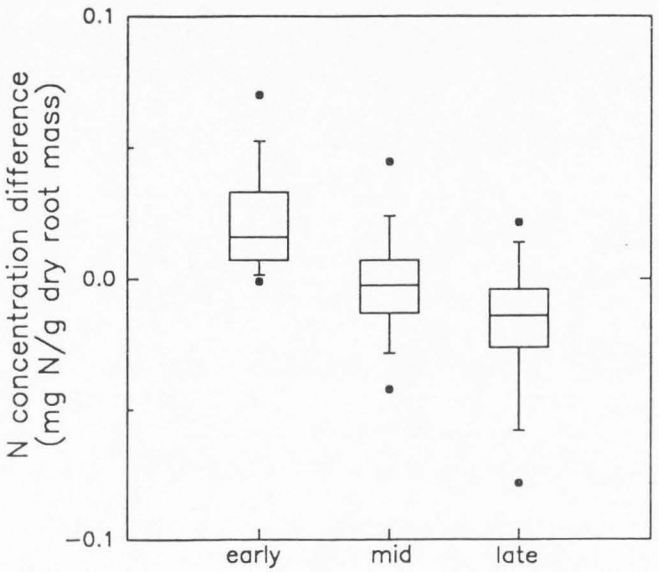

Fig. 19. Root tissue N concentration differences before and after pulses for the early-, mid-, and late-spring pulses. Each box plot represents prepulse tissue N concentration minus postpulse tissue N concentrations for each species averaged for all solution concentrations.

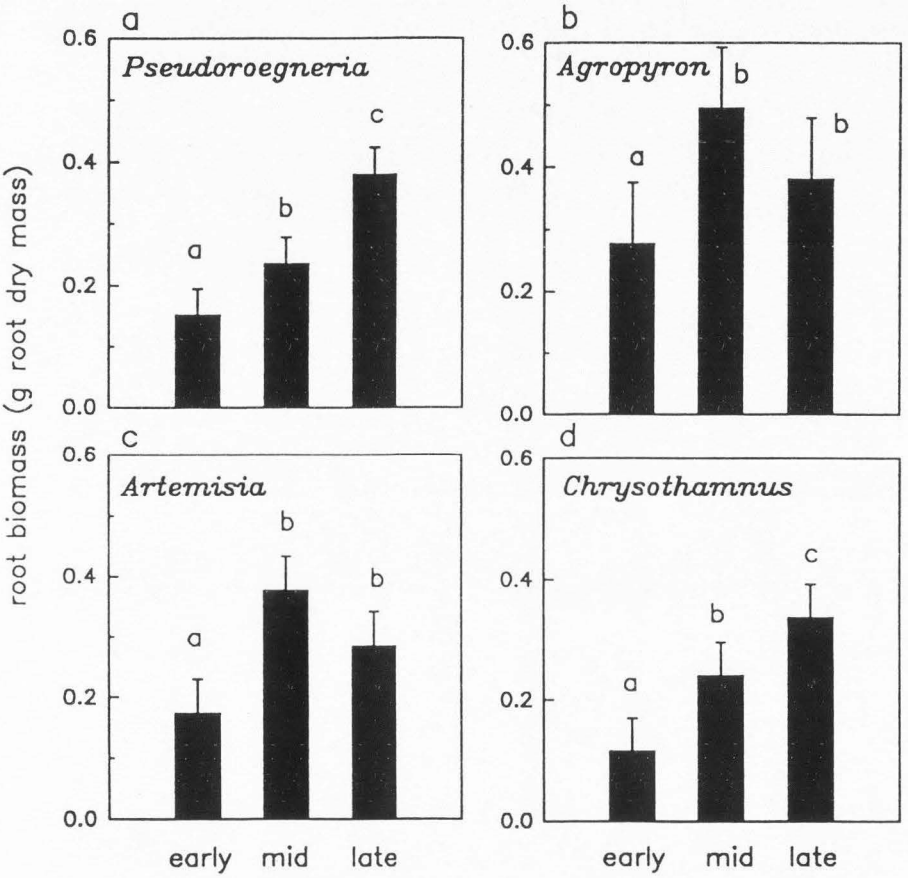

Fig. 20. Root biomass at the time of application of the early-, mid-, and late-spring pulses for a) *Agropyron*, b) *Pseudoroegneria*, c) *Artemisia*, and d) *Chrysothamnus*. Each value is the mean and one standard error from a sample size of four.

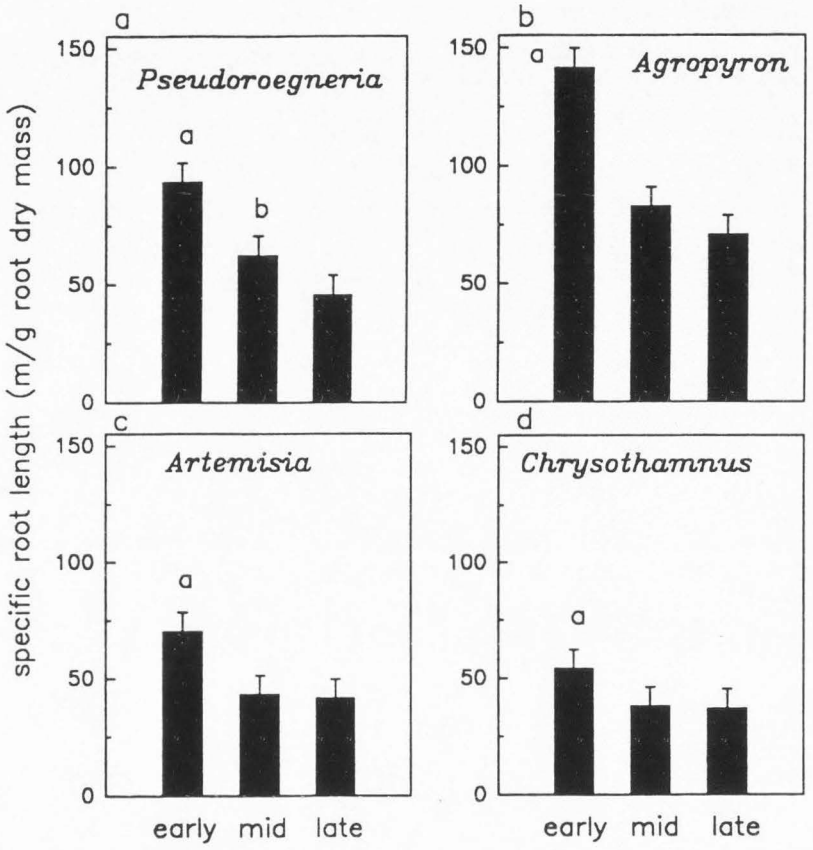

Fig. 21. Specific root length (root length per unit root mass, SRL) for fine roots at the time of application of the early-, mid-, and late-spring pulses for a) *Agropyron*, b) *Pseudoroegneria*, c) *Artemisia*, and d) *Chrysothamnus*. Each value is the mean with one standard error from a sample size of four.

CHAPTER V

SUMMARY

Plants are shaded by their neighbors at different times of the day or season, and nutrients and water fluctuate in their availability both in space and time, and yet the ability of plants to capture resources under these variable circumstances has received the attention of ecologists only recently. In this dissertation, I presented information suggesting that plants are very effective in capturing nutrients that occur heterogeneously, both in space and time. However, the ability to exploit heterogeneity in nutrient availability is variable, depending on many interacting factors such as plant phenological stage, the status of the plant, and physical factors such as soil moisture and temperature. This dissertation also demonstrated that pulsed nutrient supply is potentially important to plants, and that the importance of nutrient pulses is variable over time and among species.

In Chapter II, I tested the capacity of mature, field-grown *Agropyron desertorum* plants to exploit locally enriched patches of N by root proliferation, and how this response was affected by changes in the status of the shoot system. I manipulated shoot status by shading and fertilizing with N, and predicted that both shading and higher shoot N status would reduce demand for N and thus result in lower root growth rates in enriched N microsites as compared to unshaded plants or those with lower N status. All plants had higher root growth rates in enriched patches as compared to patches created with water and, as predicted, shoot status affected root growth rates in enriched patches. Shading reduced root growth rates by over 50%, but did not affect the timing of the response.

Surprisingly, elevated N status enhanced root growth rates in enriched patches. Previous studies comparing plants with luxury N supply to plants deficient in supply reported that plants with higher N status proliferated fewer roots than plants with lower N status (Drew and Saker 1975, 1978, Friend et al. 1990). The results from this study reflect the responses from plants along a range of nutrient sufficiency, rather than plants with surplus supply compared to plants deficient in supply. If the fertilization treatments had resulted in luxury consumption by plants and high tissue N concentrations, this field study may have corroborated results reported in studies conducted in hydroponics (e.g., Drew and Saker 1975, 1978) or with potted plants (Friend et al. 1990). However, luxury supply is unlikely to occur under field conditions, and thus, this study may be a more realistic approach to the effects of shoot N status on root growth responses to enriched nutrient microsites.

This study is one of few conducted in the field testing the ability of plants to selectively alter growth rates of part of the root system in response to enriched nutrient patches, and supports results from previous studies conducted in pots (e.g., Jackson and Caldwell 1989, Friend et al. 1990). However, one problem with this study as well as those conducted in pots is that the growing medium has been disturbed and may not be representative of bulk soil. The bulk density of the soil in these experimental systems is lower, and additionally, roots may grow at the glass-soil interface of observation windows with less impedance. Thus, this study and others document the potential of plants to proliferate roots in enriched patches, but may not completely represent responses in the

bulk soil. Results from a study by Caldwell et al. (1991) suggest that proliferation responses of roots in the bulk soil are less consistent. Thus, while this study clearly shows an effect of the shoot system on the root system, it is still necessary to determine the role of root proliferation in gaining nutrients presented in patches or pulses under true field conditions. In addition, it remains to be determined if the proliferation response occurs as a mechanism to garner nutrients in patches, or in response to nutrient uptake, and therefore after uptake. Regardless of the drawbacks discussed above, demonstrations in the field of the effect of the shoot system on root growth responses are rare in ecology. The results from this study suggest that plants that are shaded above ground by their neighbors may also be competitively disadvantaged in belowground competition for nutrients, and that plants already successfully competing for nutrients with a higher nutrient status are better able to exploit patches of nutrients than plants with lower nutrient status.

The ability of a plant to exploit soil nutrients is determined by species-specific characteristics, such as timing of growth and phenological progression. Physical factors, such as soil water and temperature, affect both nutrient availability and plant responses to nutrients. Thus, there is a complex interaction between species-specific traits and water and N availability that ultimately determines the response of an individual plant to a pulse of N. In Chapters III and IV, I presented the results from a set of experiments examining responses of Great Basin plant species to short-term pulses of N. These chapters examined the importance of pulsed nutrient supply on plant growth and productivity

during the spring growing season and the root system characters that contributed to exploiting these pulses.

In Chapter III, I measured plant growth responses and biomass production of six Great Basin species following a pulse of N applied either in the early, mid, or late spring, and compared these responses to plants grown with the same quantity of N supplied continuously. Two perennial grasses, *Agropyron desertorum* and *Pseudoroegneria spicata*, two woody shrubs, *Artemisia tridentata* and *Chrysothamnus nauseosus*, and two annual grasses, *Bromus tectorum* and *Taeniatherum caput-medusae*, were used in this study. Surprisingly, most of the species grown under the continuous supply had lower growth rates and less biomass production than plants receiving N in at least one of the pulses. The exception to this pattern was *Chrysothamnus*, which responded to all pulses and the control supply with equivalent growth rates and biomass production. Plant phenological stage was closely tied to plant responses to pulses. Of the five species that did respond to pulses, plants had their greatest response during their early growth phases when growth rates and demand were high. In addition, four of the six species had their greatest response in the early spring. Thus, this study showed that for many Great Basin species, the early spring is an important time when these cold-season adapted species are well suited to take advantage of a pulse. In addition, the combination of rapid plant growth rates and predictable pulses following snow melt would likely result in intense competition for nutrients at this time. This study demonstrated that plants are remarkably capable of utilizing pulses of N for significant gains in biomass, and that pulsed nutrients

are potentially important in natural systems.

As with all research, this study led to as many or more questions than it answered. One obvious direction is to expand from monocultures to mixed species, examining the importance of competitive interactions in gaining nutrients from pulses in the perennial system as well as the competitive interactions between invading annual grasses and the native perennials. The clear differences in biomass production measured in this study need to be extended to measurements of reproductive output, to determine if the timing of pulses affects seed production relative to a continuous supply. Another direction is to document the effects of pulsed N supply on plant N budgets, where N from pulses is allocated and how this changes during the season, and finally how different N pulses affect the amount of N stored and the amount of N lost in senescent plant tissue.

Considerable discussion in ecology concerns the differences between the hypotheses of Grime (1977, 1979) and Tilman (1982, 1988), particularly as they relate to stressful environments. Grime (1979) has argued that competition is relatively unimportant in stressful environments and that plants persist in stressful environments because they are stress tolerators. In contrast, Tilman (1988) has argued that competition is equally important across ecological gradients, although the limiting resource changes such that in unproductive environments competition is primarily below ground for nutrients and water, while in productive environments, competition is primarily above ground for light. However, Tilman's resource competition theory emphasizes average nutrient availability and does not take into account temporal fluctuations in nutrient

availability. Although data are available suggesting that competition occurs in unproductive environments (Caldwell et al. 1985, Fowler 1986), the relative roles of competition and stress tolerance in unproductive environments remain unclear. The temporal dynamics of nutrient and water availability in unproductive systems such as the Great Basin suggest that the relative importance of competition and tolerance changes over time. During times of nutrient pulses and high water availability, plants must successfully compete for these resources, and yet they must also successfully persist during periods of low resource availability. These characters may be linked by the effect of the ability of a plant to garner resources during times of high resource availability on the ability of a plant to survive periods of low resource availability.

In the Great Basin, plants must effectively compete for water and nutrients in the spring, and then survive conditions of summer drought. In this scenario, neither process alone determines plant persistence in the Great Basin, but a combination of both competitive ability and stress tolerance is important in determing community composition, and their relative importance changes through time. In this study, the importance of the timing of N availability plus the relative importance of pulsed as compared to a more constant supply indicate that temporal variability in resource availability must be taken into account when considering the importance of competitive ability and stress tolerance as plant characters that determine community composition.

In Chapter IV, I investigated the root characteristics that contributed to plant responses to uptake of N pulses by the four perennial species discussed in the previous

study. The annuals were excluded from this study because they produced insufficient biomass for excised-root N-uptake measurements. I measured root biomass, specific root length (root length per unit root mass, SRL), and root uptake capacity of excised roots. Despite considerable temperature differences and changes in plant phenological stages, root uptake capacity remained remarkably constant for all four species throughout the season and, therefore, did not explain the differences observed in the previous study. Root biomass increased during the spring growing season while the capacity to respond to pulses decreased, and therefore root biomass also did not explain seasonal patterns of pulse exploitation. In contrast, SRL was highest in the early spring and decreased throughout the spring, suggesting that the ability to effectively exploit the soil volume in the early spring is related the quantity of actively growing fine roots and their ability to effectively exploit the soil volume in the early spring.

The measurements of root uptake capacity in this study are unusual in that uptake capacity is measured at different times during the spring growing season, tracking changes in uptake capacity as the root system develops, plant demand for N changes, and plant phenology progresses. More often, uptake capacity has been measured at only one time (e.g Jackson et al. 1990), or using seedlings rather than mature plants (e.g Lee and Rudge 1986, Hole et al. 1990), and thus not providing an understanding of how these characters change through time nor how they vary for different species. The measurements of uptake capacity in this study revealed a remarkable ability to maintain homeostasis in uptake rates over a wide range of temperatures and plant phenological stages. The physiological

ability of these root systems to rapidly take up N in the early spring despite low soil temperatures, plus the presence of many actively growing fine roots, resulted in the effective capture of nutrients from early season pulses.

Although this study yielded much interesting information, it did not explicitly identify the root system characters that determined uptake capacity during the growing season. The SRL was measured only on fine roots, and not on the bulk soil root samples. Thus, my information on SRL is specific to the fine root fraction, and does not indicate an overall value of root system SRL, nor give an indication of the fraction of the root system that was fine roots. To determine this information would have required more extensive destructive sampling than was feasible in this study. The SRL is often considered to be a surrogate measurement of root surface area (Barber 1995). Because volume and thus mass increase as a function of the root radius squared, while surface area increases linearly, roots of the same weight but higher SRL have more surface area than roots with lower SRL. Because my uptake capacity measurements were on a per mass basis, it is quite likely (as discussed in Chapter IV) that changes in root surface area may contribute to the measurements of uptake capacity, particularly in the early spring. A more important point is that there is no good method for assessing the amount of root surface area that is involved in actively absorbing nutrients. Without this information, it is difficult to assess the relative importance of different root characteristics in nutrient uptake capacity under field conditions.

In summary, in this dissertation I showed that the status of the shoot system may

have a considerable effect on the ability of a plant to exploit belowground resource heterogeneity. In addition, I showed that plants are extremely effective in taking up N supplied in pulses, and that the capacity of plants to exploit N pulses changes during the course of the growing season. The pattern of response to N pulses over the course of the spring growing season was unique to each species, but there was strong evidence that the cold-season adapted species maximized N pulse exploitation in the early spring. Thus, there was little evidence for reduction in competition through temporal partitioning of N uptake. Instead, competition may be intense in the early spring. My measurements of root uptake capacity revealed a remarkable homeostasis in uptake capacity. Root uptake capacity and root biomass did not explain the differences in pulse exploitation by the perennial species. Instead, the amount of actively growing fine roots combined with the ability to exploit N pulses at low soil temperatures may explain the patterns I observed in plant responses to pulses. The responses of plants to pulsed resource supply have received little attention. My data suggest that plants are capable of using pulsed resources, that this capability varies over time, and that temporal fluctuations in resource variability may be an important factor in plant community dynamics.

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APPENDICES

APPENDIX A

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Bilbrough, Carol J. and Martyn M. Caldwell. 1995. The effects of shading and N status on root proliferation in nutrient patches by the perennial grass Agropyron desertorum in the field. Oecologia 103:10-16.

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APPENDIX B

STATISTICAL TABLES

Table 2. ANOVA of *Bromus tectorum* responses to pulse treatments from Chapter III using the General Linear Models procedure in SAS (SAS 1988). Main plots were blocked, and treatment levels are early-, mid-, and late-spring pulses.

Dependent variable: shoot mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.206025	9	0.125512	1.6415	0.25
Treatment	3	0.342525	9	0.125512	2.729	0.10
Block*Trt	9	0.125512	32	0.101129	1.2411	0.31

Dependent variable: root mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.000381	9	0.000529	0.7192	0.56
Treatment	3	0.000999	9	0.000529	1.8864	0.20
Block*Trt	9	0.000529	32	0.000357	1.4848	0.19

Dependent variable: number of tillers

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	4.25	9	9.2129	0.4613	0.72
Treatment	3	28.0833	9	9.2129	3.0482	0.08
Block*Trt	9	9.2129	32	9.0	1.0237	0.44

Table 3. ANOVA of *Agropyron desertorum* responses to pulse treatments from Chapter III using the General Linear Models procedure in SAS (SAS 1988). Main plots were blocked, and treatment levels are early-, mid-, and late-spring pulses.

Dependent variable: shoot mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	1.515569	9.08	1.964007	0.7717	0.54
Treatment	3	10.00035	9.08	1.964007	5.0918	0.024
Block*Trt	9	1.981266	15	0.669569	2.9590	0.031

Dependent variable: root mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.21533	9.37	0.348265	0.6183	0.62
Treatment	3	0.1.3808	9.37	0.348265	3.9650	0.045
Block*Trt	9	00.34578	15	0.534154	0.6474	0.74

Dependent variable: number of tillers

Source	Numerator D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	38.7763	9.25	27.7037	1.3997	0.31
Treatment	3	362.158	9.25	27.7037	13.0725	0.0011
Block*Trt	9	27.68555	15	29.06667	0.9525	0.51

Table 4. ANOVA of *Taeniatherum caput-medusae* responses to pulse treatments from Chapter III using the General Linear Models procedure in SAS (SAS 1988). Main plots were blocked, and treatment levels are early-, mid-, and late-spring pulses.

Dependent variable: shoot mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.295578	9	0.101066	2.9246	0.092
Treatment	3	1.014921	9	0.101066	10.0421	0.0031
Block*Trt	9	0.101066	32	0.052744	1.9162	0.085

Dependent variable: root mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.001405	9	0.001376	1.0208	0.43
Treatment	3	0.003862	9	0.001376	2.8066	0.10
Block*Trt	9	0.001376	32	0.000385	3.5772	0.0036

Dependent variable: number of tillers

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	25.5764	9	17.1875	1.4881	0.28
Treatment	3	102.2986	9	17.1875	5.9519	0.016
Block*Trt	9	17.1875	32	4.0208	4.2746	0.0010

Table 5. ANOVA of *Pseudoroegneria spicata* responses to pulse treatments from Chapter III using the General Linear Models procedure in SAS (SAS 1988). Main plots were blocked, and treatment levels are early-, mid-, and late-spring pulses.

Dependent variable: shoot mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.323631	9.53	0.213382	1.5167	0.27
Treatment	3	2.435476	9.53	0.213382	11.4137	0.0017
Block*Trt	9	0.210118	32	0.458145	0.4586	0.88

Dependent variable: root mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	0.002107	9.08	0.112657	0.0187	0.99
Treatment	3	0.17803	9.08	0.112657	1.5803	0.26
Block*Trt	9	0.113669	15	0.036694	3.0978	0.026

Dependent variable: number of tillers

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Block	3	18.15152	9.10	6.51983	2.7840	0.10
Treatment	3	9.75	9.19	6.462255	1.5088	0.27
Block*Trt	9	6.578	14	2.42857	2.7087	0.046

Table 6. ANOVA of *Artemisia tridentata* responses to pulse treatments from Chapter III using the General Linear Models procedure in SAS (SAS 1988). Main plots were blocked, and treatment levels are early-, mid-, and late-spring pulses. Initial plant weight is treated as a covariate (oldstem)

Dependent variable: shoot mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Oldstem	1	195.9276	8	11.00293	9.6272	0.014
Block	3	2.735556	8	11.00293	0.2486	0.86
Treatment	3	22.5086	8	11.00293	2.1457	0.15

Dependent variable: root mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Oldstem	1	9.62831	8	0.2899937	33.2018	0.0004
Block	3	0.565287	8	0.2899937	1.9493	0.20
Treatment	3	0.7134	8	0.2899937	2.4601	0.14

Table 7. ANOVA of *Chrysothamnus nauseosus* responses to pulse treatments from Chapter III using the General Linear Models procedure in SAS (SAS 1988). Main plots were blocked, and treatment levels are early-, mid-, and late-spring pulses. Initial plant weight is treated as a covariate (oldstem)

Dependent variable: shoot mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Oldstem	1	66.28632	8	7.16712	9.2487	0.016
Block	3	14.40945	8	7.16712	2.0105	0.19
Treatment	3	6.85137	8	7.16712	0.9559	0.46

Dependent variable: root mass

Source	D.F.	Mean Square	Error D.F.	Error MS	F Value	Pr>F
Oldstem	1	5.744369	8	0.996779	5.7629	0.043
Block	3	1.200294	8	0.996779	1.2042	0.37
Treatment	3	0.155373	8	0.996779	0.1559	0.92

Table 8. ANOVA for *Agropyron desertorum* root uptake rates in response to springtime nitrogen pulses. Root uptake capacity was analyzed as a split-split plot using the Mixed Procedure in SAS. Treatment was the main effect, pre- and postpulse measurements were the first split, and solution concentration was the second split. See Chapter III for additional details regarding design and methods. Mean square values are not presented for uptake capacity because Proc Mixed does not produce them.

dependent variable: net uptake rate, ambient temperatures.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	0.48	0.63
Pulse	1	9	0.0002	0.99
Trt * Pulse	2	9	7.04	0.014
Concentration	2	34	21.84	0.0001
Trt * Concn	4	34	0.06	0.99
Pulse * Concn	2	34	1.43	0.25
Trt * Pulse * Concn	4	34	1.46	0.23

dependent variable: net uptake rate, 20°C.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	1.17	0.35
Pulse	1	9	0.01	0.91
Trt * Pulse	2	9	2.41	0.14
Concentration	2	34	12.10	0.0001
Trt * Concn	4	34	1.69	0.19
Pulse * Concn	2	34	0.40	0.67
Trt * Pulse * Concn	4	34	0.60	0.62

Table 9. ANOVA for *Pseudoroegneria spicata* root uptake rates in response to springtime nitrogen pulses. Root uptake capacity was analyzed as a split-split plot using the Mixed Procedure in SAS. Treatment was the main effect, pre- and postpulse measurements were the first split, and solution concentration was the second split. See Chapter III for additional details regarding design and methods. Mean square values are not presented for uptake capacity because Proc Mixed does not produce them.

dependent variable: net uptake rate, ambient temperatures.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	1.68	0.24
Pulse	1	9	0.71	0.42
Trt * Pulse	2	9	3.82	0.07
Concentration	2	34	37.96	0.0001
Trt * Concn	4	34	2.17	0.09
Pulse * Concn	2	34	0.58	0.57
Trt * Pulse * Concn	4	34	0.28	0.89

dependent variable: net uptake rate, 20°C.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	3.82	0.063
Pulse	1	9	10.00	0.011
Trt * Pulse	2	9	6.96	0.015
Concentration	2	34	32.70	0.0001
Trt * Concn	4	34	0.97	0.42
Pulse * Concn	2	34	0.66	0.52
Trt * Pulse * Concn	4	34	0.96	0.42

Table 10. ANOVA for *Artemisia tridentata* root uptake rates in response to springtime nitrogen pulses. Root uptake capacity was analyzed as a split-split plot using the Mixed Procedure in SAS. Treatment was the main effect, pre- and postpulse measurements were the first split, and solution concentration was the second split. See Chapter III for additional details regarding design and methods. Mean square values are not presented for uptake capacity because Proc Mixed does not produce them.

dependent variable: net uptake rate, ambient temperatures.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	1.38	0.30
Pulse	1	9	0.10	0.76
Trt * Pulse	2	9	3.99	0.06
Concentration	2	34	150.96	0.0001
Trt * Concn	4	34	2.52	0.06
Pulse * Concn	2	34	0.16	0.85
Trt * Pulse * Concn	4	34	2.14	0.09

dependent variable: net uptake rate, 20°C.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	3.30	0.084
Pulse	1	9	0.00003	0.99
Trt * Pulse	2	9	1.58	0.26
Concentration	2	34	97.21	0.0001
Trt * Concn	4	34	4.28	0.013
Pulse * Concn	2	34	0.56	0.56
Trt * Pulse * Concn	4	34	1.08	0.37

Table 11. ANOVA for *Chrysothamnus nauseosus* root uptake rates in response to springtime nitrogen pulses. Root uptake capacity was analyzed as a split-split plot using the Mixed Procedure in SAS. Treatment was the main effect, pre- and postpulse measurements were the first split, and solution concentration was the second split. See Chapter III for additional details regarding design and methods. Mean square values are not presented for uptake capacity because Proc Mixed does not produce them.

dependent variable: net uptake rate, ambient temperatures.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	0.78	0.49
Pulse	1	9	0.03	0.87
Trt * Pulse	2	9	7.36	0.013
Concentration	2	34	144.29	0.0001
Trt * Concn	4	34	1.20	0.33
Pulse * Concn	2	34	3.78	0.034
Trt * Pulse * Concn	4	34	2.11	0.10

dependent variable: net uptake rate, 20°C.

Source	NDF	DDF	F Value	Pr>F
Treatment	2	9	19.60	0.0005
Pulse	1	9	0.06	0.82
Trt * Pulse	2	9	1.56	0.26
Concentration	2	34	137.05	0.0001
Trt * Concn	4	34	1.34	0.28
Pulse * Concn	2	34	0.64	0.54
Trt * Pulse * Concn	4	34	1.09	0.37

CURRICULUM VITAE

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EDUCATION

Ph.D. 1996) Rangeland Plant Ecology, Utah State University, Dr. Martyn M. Caldwell, supervisor
M.S. 1990, Range Plant Ecology, Utah State University, Dr. James H. Richards, supervisor
B.S. 1979, Zoology, University of Georgia

RESEARCH EXPERIENCE

Plant uptake of pulsed N in cold-desert shrub-grass communities (Ph.D. research)
1990-present, Graduate Research Assistant, Utah State University
Mechanisms of herbivory tolerance in Great Basin shrubs (M.S. research)
1985-1990, Graduate Research Assistant, Utah State University
Farming systems research in a subsistence agriculture system
1982-1984, Cropping Systems Extensionist, U.S. Peace Corps, Swaziland
Fisheries biology in subtropical streams and impoundments
1981-1982, Fisheries Biologist, U.S. Peace Corps, Swaziland
Nitrogen cycling in salt marsh ecosystems
1979-1981, Research Technician, University of Georgia Marine Institute, Sapelo Island

TEACHING EXPERIENCE

Guest Lecturer, Utah State University
Properties and Management of Wildland Soils 1994
International Rangeland Management 1986
Graduate Teaching Assistant, Utah State University
Natural Resources and the Future, tutorial 1985
Physiological Ecology of Plants, Practicum 1988
Plant Physiology Laboratory 1988,1989
Plant Morphology and Anatomy Laboratory 1989

Instructor, Swaziland Agricultural College
Introductory Fish Biology and Management, lecture and practicum 1981-1983
Lecturer, Swaziland Ministry of Education In-Service Training Program
Refresher course on fish biology and small-pond aquaculture 1981-1982

COMPETITIVE FELLOWSHIPS AND AWARDS

President's Fellowship, Utah State University
University of Georgia Honors Society Achievement Award

PROFESSIONAL SERVICE

Society Memberships:
Ecological Society of America
Society for Range Management
Journal Reviews:
Ecology, Ecological Monographs, New Phytologist
Organized Meetings:
Utah Plant Ecology Meetings, 1994
Graduate Student Activities:
Graduate student space coordinator 1987-1989
Graduate student representative to the faculty 1990-1991
Graduate student member of faculty search committee 1990
Graduate student-Faculty interaction committee 1994-current

PRESENTATIONS

Contributed papers:
Ecological Society of America 1987, 1993, 1994, 1995
Society for Range Management 1988
Utah Plant Ecology Meetings 1986, 1989, 1990, 1994
Contributed posters:
Ecological Society of America 1990, 1994
Botanical Society of America 1991, 1992
Society for Range Management 1989

PUBLICATIONS

Peer-Reviewed:

Bilbrough, Carol J., Sara E. Duke, and Martyn M.Caldwell. The role of root biomass and root uptake capacity in exploitation of N pulses by four Great Basin species. Submitted to

The American Journal of Botany.

Bilbrough, Carol J. and Martyn M. Caldwell. Exploitation of springtime ephemeral N pulses by six Great Basin Plant species. Submitted to Ecology

Bilbrough, Carol J. and Martyn M. Caldwell 1995 The effects of shading and N status on root proliferation in nutrient patches by the perennial grass *Agropyron desertorum* in the field. Oecologia 103:10-16.

BassiriRad, Hormoz, Martyn M. Caldwell, and Carol J. Bilbrough. 1993 Effects of soil temperature and nitrogen status on kinetics of $^{15}NO_3^-$ uptake by roots of field-grown *Agropyron desertorum* (Fisch. ex Link) Schult. New Phytologist 123:485-489.

Bilbrough, C.J. and J.H. Richards. 1993 Growth of sagebrush and bitterbrush following simulated winter browsing: Mechanisms of tolerance. Ecology 74:481-492.

Bilbrough, C.J. and J. H. Richards 1991 Branch architecture of sagebrush and bitterbrush: use of a branch comples to describe and compare patterns of growth. Canadian Journal of Botany 69:1288-1295.

Non Peer-Reviewed Publications

Bilbrough, Carol J. 1982 Basic Fish Biology and Aquacultural Techniques. Manual for high school agriculture teachers. Swaziland Ministry of Education In-Service Training Program.